THE UNIVERSITY OF ALBERTA

A QUANTITATIVE GENETIC ANALYSIS OF AVOIDANCE

BEHAVIOR IN MUS MUSCULUS

by

C

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A Quantitative Genetic Analysis of Avoidance Behavior in Mus musculus submitted by Takako Mary Holmes in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

Analyses were performed on a measure of avoidance behavior in four inbred strains, A/HeJ, BALB/cJ, SWR/J, and 129/J, of Mus musculus and their F_1 and F_2 reciprocal crosses and the first generation of backcrosses to the inbred strains. The results indicate a difference between males and females with female offspring scoring a significantly higher number of correct avoidances. In general maternal effects were absent. The overall mode of inheritance is that of dominance with males showing more overdominance than females. Examination of individual crosses shows that the mode of inheritance varies with the strains considered.

Non-allelic and genotype-environment interactions were found to be present. Transformations were applied with no improvement in the adequacy of scale. The difficulty stems from the large variances obtained for certain crosses in the F_1 diallel cross. The presence of non-allelic interaction may be responsible for inflation of dominance.

Testing was carried out for three consecutive days with genetic effects being more pronounced on day one. The variation due to dominance effects is strongest on day one and decreases further on days two and three.

ACKNOWLEDGEMENTS

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INTRODUCTION

Within the field of behavior genetics, analysis
can progress through three major steps. Step one, which is
establishing that genetic factors play a part in the behavior
studied, is usually a comparison of inbred strains or a
selection study. Step two is generally a quantitative
analysis as the behavior studied is most probably controlled
by a polygenic system, and step three is manipulation of
genotypes at the level of genes, chromosomes, gametes, or
populations. Reviews have been carried out by Benzer (1971),
Hirsch (1967), Lindzey & Thiessen (1970), Manosevitz, Lindzey,
& Thiessen (1969), and Wahlsten (1971). The particular level
one works at depends on both the organism and the behavior
chosen for study. The behavior which this thesis deals
with is avoidance conditioning in inbred strains of the
house mouse, Mus musculus, and analysis is still at step two.
Although the mouse is a suitable mammal for genetic manipul-
ation, the amount of information known about the learning
behaviors usually studied is not sufficient to proceed to
step three.

The essence of avoidance conditioning is that the
organism must learn to make a response in order to avoid an
impending occurrence of noxious stimulation. Kimble (1961),
in considering conditioning in historical perspective, states
that its uncritical acceptance by psychologists was primarily
due to Bekhterev although the details were Pavlov's.

He states that its enthusiastic acceptance was due to its seemingly objective methods and general applicability. Since then it has become apparent that there are many complex features involved.

Two forms of conditioning are distinguishable: classical and instrumental conditioning. Classical conditioning basically involves an unconditioned stimulus (UCS) which reliably produces an unconditioned response (UCR) and a conditioned stimulus (CS) that does not produce the UCR. The CS and UCS are repeatedly paired and a response similar to the UCR develops to the CS. This response is called the conditioned response (CR). It should be noted that the UCR and CR are not exactly the same. It is generally agreed that they are quantitatively different (Kimble, 1961; Marx, 1969).

Instrumental conditioning is based on Thorndike's "law of effect" which states that a response is strengthened if it is followed by satisfying consequences and weakened if it is followed by dissatisfying consequences. It involves response contingent reinforcement and does not involve choice among experimentally defined alternatives (Kimble, 1961; Marx, 1969).

The main differences between classical and instrumental conditioning are: (1) an UCS is not present in instrumental conditioning to elicit the to-be-learned response, and (2) in instrumental conditioning the reinforcement is dependent upon the subject's behavior, whereas reinforcement is given in classical conditioning regardless of the subject's behavior. Examples of both types of conditioning can be found in Marx (1969).

The traditional explanation for avoidance conditioning is a two-process learning theory advocated by Mowrer (1947,1956) and Solomon & Wynne (1954). They propose that on the basis of the pairing of neutral and noxious stimuli, a motive of 'fear' is acquired early in training to the previously neutral and now 'feared' stimulus. Responses leading to the removal of the 'feared' stimulus are strengthened by a drive-reduction mechanism of reinforcement. The two processes involved are:
(1) classical conditioning - association learning which leads to the establishment of a motivational state known variously as fear, anxiety, or conditioned aversion, and (2) instrumental conditioning - law of effect learning which enables the animal to reduce the motivational state. This can be presented as:

```
UCS ─────────────────────► UCR
(shock)                    (anxiety)
  ⋮

CS── UCS ─────────────────► UCR

  .
  ⋮

CS ───────────────────────► CR
(buzzer)                   (anxiety)
                        ► RUNNING ──────────►REINFORCEMENT:
                                             drive-reduction
```
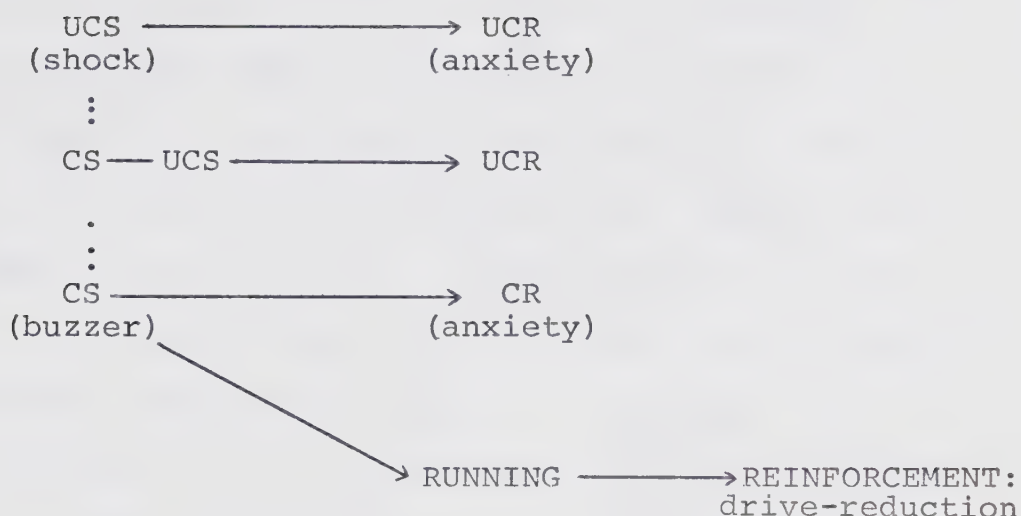
Bolles (1970) stresses the importance of the
particular avoidance response studied and suggests that an
avoidance response will be rapidly acquired only if it is
an innate defense reaction in the animal's repertoire,
which he labelled a "species-specific defense reaction".
He proposes that the learning mechanism is the suppression
of ineffective species-specific defense mechanisms. More
slowly acquired avoidance responses may not be species-
specific defense reactions and they may have different
mechanisms operating.

Herrnstein (1969) and Bolles (1970), in reviewing
the literature on avoidance learning indicated the confusion
and complications involved in generalizing over behaviors
and species. No final generalization can be made regarding

the theory of avoidance conditioning. Nor can a final
decision be reached on the role of the CS. Possible
hypotheses are: (1) that the termination of the CS is
assumed to lead to a reduction of fear which in itself is
reinforcing (the hypothesis suggested above (Mowrer, 1947,
1956; Solomon & Wynne, 1954)), (2) that strictly by the
pairing of the CS with shock and by disregarding any emotion,
the CS becomes a conditioned negative reinforcer, or
(3) that termination of the CS provides information feed-
back, that is, CS termination tells the animal that shock
is not going to occur and this is positive reinforcement.

LITERATURE REVIEW

Strain Differences

Strain differences in avoidance conditioning in
inbred strains of mice have been shown by King and
Mavromatis (1956); Royce and Covington (1960); Collins (1964);
Carran, Yeudall and Royce (1964); Royce (1966,1972); Bovet,
Bovet-Nitti and Oliverio (1966,1969); Winston and Lindzey
(1967); Schlesinger and Wimer (1967); Oliverio (1967);
Zerbolio (1967); Wimer (1970); Rose and Parsons (1970);
Royce, Yeudall and Poley (1971); and Oliverio, Castellano
and Messeri (1972). Scudder, Avery and Karczmar (1969)
found differences in five genera of mice including three
inbred strains of Mus musculus.

In contrast with Bovet, et al (1966,1969) and
Oliverio, et al (1972), van Abeelen (1966) and Schlesinger
and Wimer (1967) did not find significant differences
between C57Bl/6J and DBA/2J mice. Royce and Covington (1960)
reported strain differences between C57Bl/6J's and an
unspecified DBA strain, and found that more than half of the
C57Bl/6J mice did not meet the criterion of five successive
conditioned responses within 700 trials. Royce and
Covington (1960) found two other strains, C57BR/cd and A/J,
to be slow conditioners by their procedures in contrast to

Bovet, et al (1966,1969) who found C57BR/cd mice to be among
the highest level of avoiders and A/J's to be intermediate.
Schlesinger & Wimer (1967) and Collins (1964) found A/J's to
be poor and intermediate, respectively. These discrepancies
can be explained by the vastly different experimental
procedures used by the different authors as shown in Table 1.

Bovet, et al (1968,1969), in studying massed
versus distributive learning schedules within sessions and
over sessions, have shown that there is an optimal schedule
depending on the strain considered. In the three strains
analyzed they found C3H/He mice perform best when the trials
are massed, DBA/2J mice perform best when the trials are
spaced, and BALB/c mice are characterized by an intermediate
pattern which is independent of the training schedule.
Wimer (1970), in comparing massed versus distributed trials
in DBA/2J and C57Bl/6J mice, found DBA/2J mice show superior
learning performance when trials are massed and C57Bl/6J
mice do better when trials are distributed. The contrad-
ictory results regarding DBA/2J mice may be due to the fact
that Wimer studied the effect of learning schedule on six
trials, whereas, Bovet, et al studied the effects on 200
and 250 trials. Learning patterns in other inbred strains
of mice have not been reported.

Author	Apparatus	CS	UCS	US-UCS Interval	CR	ITI	Number of Trials	Age in days
Bovet, et al (1966,1969); Bovet-Nitti, et al (1969); Oliverio, et al (1972)	shuttle-box (2 compartment cage)	lamp (10W)	unspecified shock	5 sec	running into the other compartment	5 sec	100 for 5 days	unspecified
Carran, et al (1964)	shuttle-box 15¼ x 3¼ x 1½ inches	buzzer	variable shock	5 sec	crossing the midline	120 sec	25 / day until 5 successive CRs	40 - 50
Collins (1964)	shuttle-box 26¼ x 5 x 4 cm	3000 cycle/sec buzzer	unspecified shock	2.5 sec	jumping across a charged pit	30 sec	200	100
Denenberg (1958)	box 3¼ x 7.75 x 10 inches	buzzer	480 V 0.5 mA	variable	variable-jump run,walk,etc.	41 sec	10	variable
King, et al (1956)	Licklider gridless wireless rat shocker	door buzzer	unspecified shock	2.2 sec	jump a 2 inch hurdle	3 sec	30 / day for 10 days	97 - 127
Rose, et al (1970)	perspex box with a grid floor	light	60 V 250 mA	2 sec	jump a low central barrier	60 sec	4 / 1 hr rest/ 3/ 24 hr rest/3	59
Royce, et al (1960)	same as Carran, et al (1964)	buzzer	0.3 mA	0.5 sec	run to the other side	10 sec	700 or until 5 successive CRs	30 - 51
Royce, et al (1971); Royce (1972)	same as Carran, et al (1964)	tone buzzer	400 V	3 sec	run to the other side	120 sec	25/ 3 days 25/ 4 days	40 ± 3
Schlesinger, et al (1967)	7 x 6.75 x 6.75 inch box with an escape shelf	buzzer and light (100W)	0.8 mA 340 V	0	jumping to a shelf	15 - 30 sec	50 or 8 CR in 10 trials	60 ± 3
Scudder, et al (1969)	inclined ramp with 5 chambers	door closed	1.3 mA 800 V	5 sec	climbing	0	10	?
van Abeelen (1966)	jumping box 6¼ x 6¼ x 6 inches	forced on grid	0.13 mA to 0.20 mA	15 sec	jump onto shelf	30 sec	3	90 - 145
Wimer (1970)	jumping box	forced on grid	unspecified shock	?	jump onto shelf	1 min or 24 hours	6	?
Zerbolio (1967)	wheel	4000 cps 67-78 dB tone	1.5 mA	5 sec	¼ of a wheel turn	20 - 60 sec	50 for 8 days	40

ITI = intertrial interval
V = volts, mA = milliamps

Table 1: Apparatus and conditioning parameters used by various authors.

Table 2 lists the mean percent avoidance or mean trials to meet an arbitrary criterion for studies involving more than two strains. Table 3 shows the Pearson product-moment and Spearman rank-order coefficients of correlation between studies which had more than three strains in common. Comparisons between studies using the two different measures, mean percent avoidance and number of trials to meet a specified criterion, are based on the untested assumption that the faster an animal reaches the criterion, the more avoidance responses it will make. Between authors the agreement is poor but studies conducted by the same authors are very highly correlated. Henderson (1970) has pointed out the possibility that early environmental interactions with genotype may limit the validity of findings to each unique laboratory situation. Possible explanations for the discrepancies between authors are: (1) different apparatuses, different conditioned stimuli, conditioned responses, shock levels, intertrial and CS-UCS intervals; and (2) different training schedules (See Table 1).

In summary, it is evident that using the same apparatus and parameters, consistent strain differences in avoidance conditioning in inbred strains of mice are found. There appears to be more variation than expected in avoidance conditioning behavior within the genetically similar lines derived from the same family.

	Collins (1964)	Bovet, et al (1966)	Bovet, et al (1969)	Oliverio, et al (1972)	Royce, et al (1971)	Royce (1972)	Royce, et al (1960)	Royce (1966)	Schlesinger, et al (1967)	Carran, et al (1964)	
										100 V	400 V
DBA											
DBA/1	37(I)						125(H-I)				
DBA/2		49	52(H)	40		55(I)		31	22(H)		
C3H	47(H)						73(H)	38		24	19
C3H/He		5	10(L)			64(I)			26(I)		
CBA		1	3(L)								
A/J	32(I)	36	29(I)				N/C(L)		43(L)		
A/HeJ		27	25(I)		70(H)	83(H)			36(L)		
BALB/c	8(L)	24	29(I)		42(I-L)	48(L)	137(I)	128	34(L)		
C58					64(H)	78(H)	209(I)			48	18
C57Bl/J									14(H)		
C57Bl/10	43(H)	34	34(I)								
C57Bl/6		6	11(L)	7			N/C(L)		14(H)		
C57BR/cd		59	48(H)			73(H-I)	N/C(L)				
SEC/1ReJ				53							
SWR/J					69(H)	85(H)	51(H)			15	19
129/J					38(I-L)	50(I-L)		24			
SWISS		25									
AKR/J					47(I)	47(I)	N/C(L)				

<u>Mean Percent Avoidance</u>   <u>Mean Trials to Criterion</u>

V=volts
H = high
I = intermediate
L = low
N/C = not conditionable

Table 2: Scores obtained by authors using more than two strains.

	Royce (1971)	Schlesinger (1967)	Bovet (1969)
Bovet (1966)	0.15 (5)	0.38 (6)	0.97***(9)
Bovet (1969)	0.13 (5)	0.17 (6)	
Royce (1972)	0.99***(6)		

	Royce (1971)	Schlesinger (1967)	Bovet (1969)
Bovet (1966)	-0.08 (5)	-0.31 (6)	0.93**(9)
Bovet (1969)	-0.50 (5)	-0.19 (6)	
Royce (1972)	0.89*(6)		

*** $p < 0.005$

** $p < 0.01$

* $p < 0.05$

( )   number of strains used in the correlations

Table 3:   Matrices of between study correlations.

   (Upper table is the matrix of Pearson product-
   moment correlations; lower table is the matrix
   of Spearman rank-order correlations)

Effect of Age of Testing

Denenberg (1958,1960) tested C57Bl/10 mice at 17 different age levels ranging from 13 to 150 days of age. He found 20-day old mice to be the most effective learners with a decline in learning ability as age increased to 50 days. At 100 days, the next age level studied, there was a somewhat smaller peak and a decline as age increased to 150 days. Denenberg (1960) concluded that a number of physiological processes which change with age are interacting with the conditioning procedure.

Bovet, et al (1969) studied differences in the learning and retention curves in DBA/2J mice at four different ages: 21, 60, 180, and 360 days, during sessions of 400 trials for five days, This procedure was very different from Denenberg's (1958,1960) who considered only 10 trials in one testing session. Bovet, et al's 60-day old mice showed the best performance when compared to younger or older animals. Variations of responding were evident between two consecutive sessions. No decline in percent avoidance occurred between sessions in the 60-day old mice, whereas, decline occurred in younger and older mice.

These studies on the effect of age on conditioning involved only one strain per study and it is therefore difficult to make general conclusions. It appears that the

effect of age will be dependent on the interaction of the processes involved in age change with the strain, apparatus, and procedure used.

Effect of Litter Size

Bovet-Nitti, Oliverio & Bovet (1969) studied avoidance learning in BALB/c mice raised singly or with siblings. They compared 15 litters with four to eight littermates with 15 litters which had been reduced to one pup within three days of birth. They found the singly raised mice to be significantly better than the sibling group and concluded that the 'mother-infant' relationship seemed to be more important than those between sibs of the same litter. The mice raised singly were significantly heavier, 20.6 grams versus 19.3 grams, than the sibling group ($p < 0.05$). Royce, Poley & Yeudall (1972), in a factor analytic study of 15 factors of emotionality, found that litter size loaded only on the avoidance conditioning factor. This analysis, based on the matrix of intercorrelations of many test scores, is used to determine the number of dimensions the tests describe. One factor or dimension was identified as an avoidance conditioning factor and litter size was found to fall on this factor.

Effect of Conditioning Parameters

Carran, Yeudall & Royce (1964) measured the rate of avoidance conditioning at five levels of shock on slow (C58) and fast strains (SWR, C3H). As voltage level increased from 40 to 400 volts, the large differences in conditioning rates disappeared. The standard deviations also decreased as voltage increased. Royce (1966) found no significant differences between BALB/c, a slow strain, and C3H mice when amperage was changed from 0.15 to 0.40 milli-amps or between C58 and C3H mice when voltage was changed from 250 to 300 to 400 volts.

Royce (1966) also varied the CS-UCS interval from two to eight seconds and intertrial interval from 30 to 180 seconds. Varying the CS-UCS interval had little effect. A three second CS-UCS interval was chosen as optimal because maximal conditioning rates with the largest strain differences were obtained using this interval. Although no significant differences were found as intertrial interval increased, the trend was toward a continued slight increase in conditioning rate as intertrial interval was lengthened. An intertrial interval of 120 seconds was chosen as optimal as the differences between C58 and C3H mice were greatest at this level. Based on a limited number of strains, optimal values were chosen within which changes in the stimulus conditons within a narrow range had relatively little effect.

The Genetics of Avoidance Conditioning

The diallel analyses by Collins (1964) and Royce,
et al (1971) agree in showing an overall dominant mode of
inheritance of avoidance conditioning with several crosses
showing overdominance. Van Abeelen (1966) found the F_1 of
DBA/2J and C57Bl/6J to be superior in avoidance conditioning
to the parental strains, and Rose & Parsons (1970) also
found the F_1's of BALB/c, C3H and C57Bl to be overdominant.
Wilcock's (1969) reanalysis of Collin's data by analysis
of variance-covariance indicates that the fast conditioning
strains are overdominant. Royce, et al (1971) using the
same analysis found complete dominance. Oliverio, Castellano
& Messeri (1972) using SEC/lReJ, DBA/2J and C57Bl/6J suggest
that almost complete dominance was the overall mode of
inheritance for avoidance behavior. This difference may be
due to the different procedures used, as noted in Table 1,
and in the different selection of strains used.

Wilcock's (1969) reanalysis suggests a major gene
effect since one strain, BALB/c, is located near the extreme
recessive end of the regression line and the remaining four
strains are clustered near the dominant end. Data by Royce,
et al (1971) confirms that BALB/cJ mice are recessive but
the remaining five strains used are distributed along the
regression line, suggesting a polygenic system rather than
a single gene effect. Oliverio, et al (1972) estimate a

minimum of three segregating units which control avoidance
behavior in the three strains which they analyzed. This
difference may be due to a different selection of strains
as the BALB/c strain was the only strain in common in the
Collins (1964) and Royce, et al (1971) studies; and no
strains were in common with the Oliverio, et al (1972) study.

Collins (1964) found no reciprocal differences
when testing for effects of early maternal environment.
Bovet-Nitti, Bovet & Oliverio (1968) confirm this finding
in showing that the usual patterns of avoidance behavior
were not affected by cross-fostering two inbred strains of
mice, DBA/2J and C3H/He. Royce, et al (1971) found some
significant maternal effects mainly involving three strains.

Using an extension of Griffing's (1956) combining
abilities analysis of variance, Collins (1964) found both
general and specific combining ability and dams x sires
interaction to be highly significant, indicating that certain
genotypes scored significantly differently from an expect-
ation based on observed additive effects of the parental
genes. Royce, et al (1971) reported the variance due to
the additive effects of the genes and the variance due to
the dominance effects of the genes to be almost equal. This
would give support to intra-locus interaction rather than
inter-locus interaction.

Both Collins (1964) and Royce, et al (1971) report
superior conditioning for females. In Collins' study the
reciprocals x sex interaction was not significant, indicating
that avoidance conditioning is not affected by sex-linkage.
Both authors relate their data to Bruell's (1964,1967) theory
that only quantitative polygenic traits which were biolog-
ically adadptive and under past selection would exhibit heter-
otic inheritance, and that traits which possessed negligible
adaptive value would be inherited in an intermediate manner.
This is assuming adaptedness to a given environment which
has not drastically changed. Both Collins (1964) and Royce,
et al (1971) suggest that rapid avoidance conditioning would
confer a selective advantage on the species. Royce, et al
hypothesize that the sex differences are explanable in terms
of this evolutionary theory in that avoidance of noxious
stimuli as an adaptive character is more important for
females whose safety is directly related to the survival of
the offspring. Falconer (1960) states that traits most
closely related to fitness will be left with the least
amount of additive variation. Since there is a reasonable
amount of variation due to additive gene effects as
evidenced by the significance of general combining ability
in Collins' (1964) data and by the roughly equal amounts of
additive and dominance components of variation in Royce, et
al's (1971) data, it would seem that avoidance conditioning
is only one of the adaptive characteristics of the mouse.

Another possibility is that avoidance behavior may be counterbalanced by other behaviors, for example, curiosity.

Evidence concerning more specific genetic mechanisms is limited; however, van Abeelen (1966) associated the short-ear, "se", locus with avoidance conditioning, basing his findings on a comparison of mutant (se/se) with non-mutant (se/+) mice of the co-isogenic stock SEC/1Gn. Denenberg (1959) found differences in avoidance behavior in two substrains of C57Bl/10 mice which had been separated for more than 15 generations of inbreeding. He suggests that a behavioral mutation occurred which affects learning ability.

In summary, this review makes it obvious that only minimal genetic information is known about avoidance conditioning behavior in inbred strains of mice. Investigation to date has consisted of only one study (Oliverio, et al, 1972) on segregating generations. This thesis attempts to quantitatively analyze both segregating and non-segregating generations in an attempt to provide more detailed information of a quantitative genetic nature.

METHOD AND MATERIALS

Data were obtained on experimental mice bred at the University of Alberta from the inbred strains, A/HeJ, BALB/cJ, SWR/J, and 129/J, obtained from the Jackson Laboratory, Bar Harbour, Maine. The four inbred strains used are the result of over 50 generations of inbreeding by sister-brother matings and none of the inbred strains used are closely related.

Analyses were performed on the F_1 and F_2 diallel tables which are the result of all possible combinations of the parental strains (Aksel & Johnson, 1963; Hayman, 1954a, 1954b; and Griffing, 1956). Also various combinations of crosses from the first and second filial generations and the first backcross generation were analyzed. The data had been gathered by Dr. J.R. Royce, Department of Psychology, as part of a broader behavior-genetic program. However, the author bred and tested an additional 202 subjects in order to increase sample sizes in the backcrosses to both the male and female 129/J strain.

Analyses were performed on selected data, that is, not all subjects were used in each analysis. However, the specific crosses and their sample sizes are as follows: F_1 diallel table (N = 470); F_2 diallel table (N = 13333); the backcross generation from crossing the above F_1's with pure strain females (N = 559).

Apparatus

The apparatus, devised by Yeudall, Royce & DeLeeuw (1968) and shown in Figure 1 is an electronically controlled avoidance conditioning apparatus which uses an electronic buzzer for the CS and foot shock for the UCS. The CS-UCS interval, the length of UCS and intertrial interval are automatically controlled and the number of errors and the number of crossings over the midline during intertrial rest period are automatically recorded.

The apparatus consists of a shuttle-box, three and one-half inches wide, one and five-eights inches high and fifteen and one-half inches long, mounted inside an insulated chamber with a one-way mirror in the door. Photo-electric cells are mounted to focus across the midline of the shuttle-box and a speaker is located at each end below the shuttle box. The chamber is illuminated by a six watt fluorescent light bulb and is ventilated by a fan. The control unit is located in a separate room.
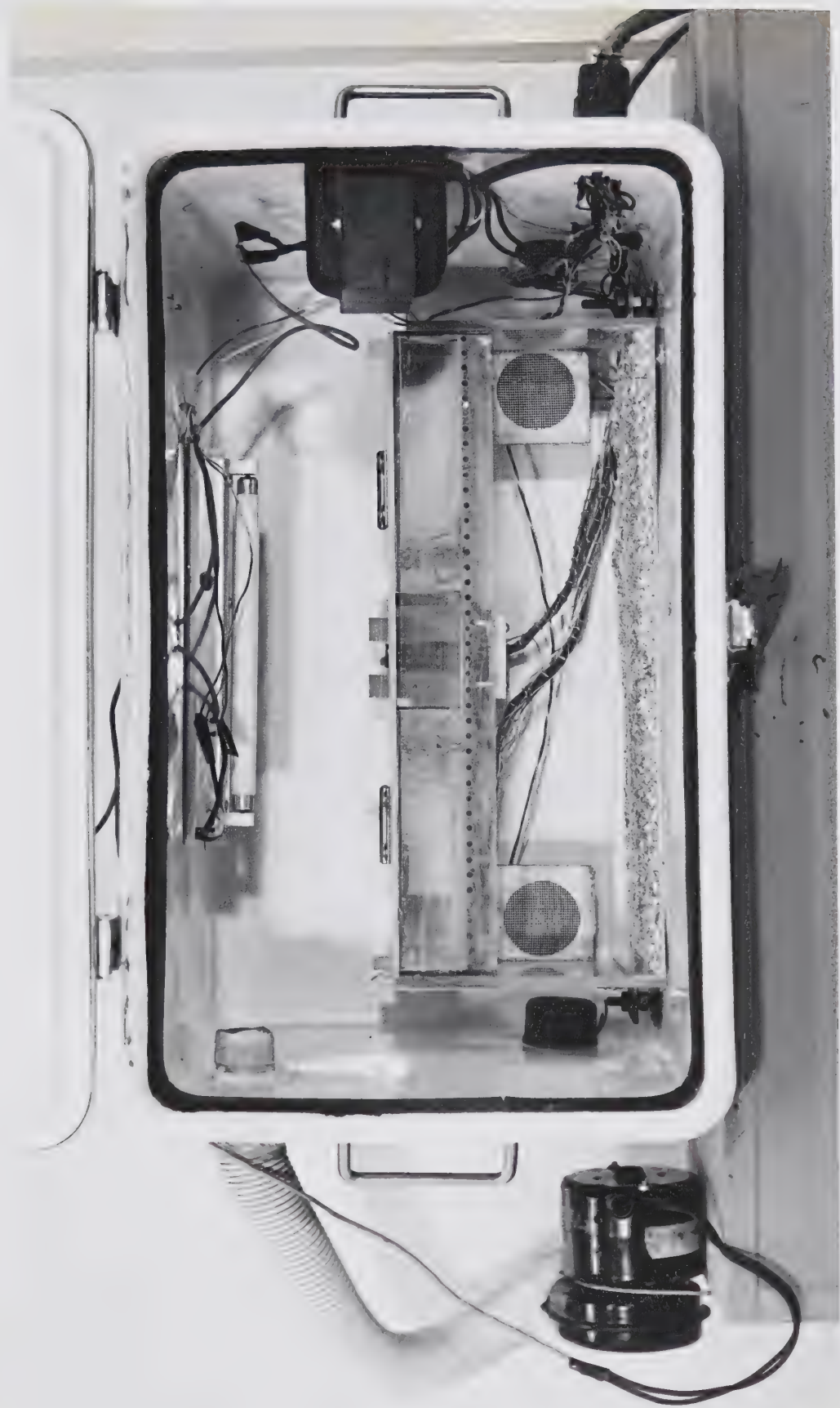
Figure 1: Avoidance conditioning apparatus.

Procedure

The subjects were raised in the laboratory according to standard procedure. A light cycle with lights on at 9:30 am and off at 9:30 pm was maintained for the entire study. All testing was carried out during the hours that lights were on. Subjects were weaned at 21 days and remained with their litter mates (maximum of five to a cage) until 33 days of age at which time they were separated into individual metal cages. Testing began at 40 ± 3 days of age.

Royce (1966) determined an optimal set of criteria for the avoidance conditioning apparatus to maximize strain differences in five inbred strains. SWR/J and BALB/cJ strains are the only strains in common with the present study. These criteria which were used are: CS-UCS interval of three seconds, intertrial interval of 120 seconds, and shock level of 400 volts.

Day one of testing consisted of a five minute adaptation period in which the subject was placed in the lighted chamber with all other controls inactive. On day two, a pre-conditioning session was conducted in which the subject was presented with five trials of CS without UCS, followed by five trials of UCS without CS. Twenty-five conditioning trials were then given. An avoidance conditioning trial is illustrated in Figure 2.

0"   3"   123"

CS   UCS   end of
on side of   trial
apparatus on
which mouse is
located

(1) If subject does not cross the midline within three seconds after onset of CS, it receives shock and an incorrect response is recorded.

(2) If subject crosses the midline before three seconds, it avoids shock.

(3) If it returns back across the midline before the three seconds is over, it will receive shock and an incorrect response will be recorded.

Figure 2: An avoidance conditioning trial.

Day three and four each consisted of twenty-five condition-
ing trials. The two measures taken were the number of
correct avoidances and the number of crossings over the
midline during the intertrial interval.

RESULTS

This section begins with an evaluation of the adequacy of scale followed by three analyses: (1) factorial analysis, (2) Hayman's diallel analyses, and (3) Mather's classical analysis.

The mean number of correct avoidance responses and the cell variances for the F_1 and F_2 diallel crosses and their array covariances, variances and differences are presented in Appendix I. The correlations of the means with the variances and the standard deviations, the probability of the Bartlett-Box homogeneity of variance M statistic, and the F_{max} ratio for the F_1 diallel table are given in Table 4. The two tests for homogeneity of variance, F_{max} and Bartlett-Box, differ in that the F_{max} ratio tests the significance of the largest to smallest variance, whereas the Bartlett-Box test is based on all the variances. Table 5 gives the corresponding values for the males and females analyzed separately. It can be seen that the relationship between the means and the measures of dispersion are different for each of the sexes, and that there is high heterogeneity of variance.

All animals were subjected to the same physical environmental conditions and therefore the variances of the cells in the F_1 diallel table should not be different from each other as the only source of variance for these genotypes

	Day 1	Day 2	Day 3	Total
Correlation between means and variances	0.141	-0.609^{*}	-0.769^{**}	-0.589^{*}
Correlation between means and standard deviations	0.257	-0.593^{*}	-0.795^{**}	-0.618^{*}
Bartlett-Box M	53.57 (p=0)	42.48 (p=0)	79.01 (p=0)	57.46 (p=0)
F_{max}	9.12^{**}	5.34^{**}	10.34^{**}	6.61^{**}

**   p<0.01
*   p<0.05

Table 4:   Relationship between means and dispersion measures
and tests of homogeneity of variance
when sexes are combined.

For MALE data	Day 1	Day 2	Day 3	Total
Correlation between means and variances	0.684^{**}	0.030	-0.472	-0.074
Correlation between means and standard deviations	0.679^{**}	0.092	-0.534^{*}	-0.098
Bartlett-Box M	49.01 (p=0)	30.55 (p=.01)	45.01 (p=0)	35.34 (p=0)
F_{max}	17.71^{**}	11.68^{**}	13.70^{**}	15.03^{**}

For FEMALE data	Day 1	Day 2	Day 3	Total
Correlation between means and variances	0.253	-0.537^{*}	-0.708^{**}	-0.583^{*}
Correlation between means and standard deviations	0.324	-0.590^{*}	-0.719^{**}	-0.649^{**}
Bartlett-Box M	27.52 (p=.03)	40.18 (p=0)	43.27 (p=0)	42.13 (p=0)
F_{max}	11.33^{**}	14.00^{**}	8.19^{**}	11.24^{**}

** $p < 0.01$
* $p < 0.05$

Table 5: Relationship between means and dispersion measures and tests of homogeneity of variance.

is that due to environment. The following transformations were performed on the F_1 diallel cross data to attempt to reduce the diverse variabilities:

$$(1) \quad X' = \frac{1}{L_1 - L_2} \times \log \left[\frac{X - L_1}{L_2 - X} \right]$$

where X = raw score (the number of correct avoidances)

    X' = transformed score

    L_1 = lower limit

    L_2 = upper limit

$$(2) \quad X' = \log(X + a/b)$$

where a = the intercept of the regression line of. the standard deviation on the mean

b = the estimated regression coefficient

$$(3) \quad X' = \sqrt{X'' + 0.5}$$

where X" = 25 - X   (the number of incorrect responses)

$$(4) \quad X' = \sqrt{X''} + \sqrt{X'' + 1}$$

$$(5) \quad X' = 2 \times \text{Arcsin} \sqrt{\frac{X''}{25}}$$

$$(6) \quad X' = \log_{10}(X'' + 1)$$

Table 6 gives the F_{max} ratios for the various transformations applied to the data. The F_{max} ratio is reduced by some of the transformations but no transformation was found which would change the F_{max} ratio to a level of non-significance.

Another test given in Wright (1952), based on Laplace's principle that a variable compounded additively of many small independent contributions shows an approximately normal distribution, irrespective of the nature of the frequency distributions of the separate units, was carried out. This involves plotting the inverse probability integral of the cumulative sum, p, of the percentage frequencies up to each class limit against X or any X'. The fact that there was crossing of lines at more than one point indicates that there is either an unresolvable interaction or the fundamental conditions for normality on an additive scale do not hold in at least one of the cases. The graphs for days one, two and three are presented in Appendix II.

	Day 1	Day 2	Day 3	Total
Raw data	3.47	4.08	4.36	4.58
$\dfrac{1}{L_1 - L_2} \times \log\left[\dfrac{X - L_1}{L_2 - X}\right]$	3.5	4.5	5.5	6.0
$\log(X + a/b)$	3.0	4.8	5.5	5.5
$\sqrt{X'' + 0.5}$	4.92	2.78	2.66	3.03
$\sqrt{X''} + \sqrt{X''+1}$	5.05	2.95	2.23	3.23
$2 \times \text{Arcsin}\sqrt{X''/25}$	2.70	4.41	4.62	5.66
$\log_{10}(X''+1)$	10.05	3.96	2.45	3.67

Table 6: F_{max} ratios for the raw data and its transformations.

(Data collapsed over sexes and reciprocals)

Factorial Analysis

A factorial analysis was carried out in which the
genetic effects of dam and sire could be evaluated independ-
ently of each other. The third main effect, sex of offspring,
and all possible interactions were also tested. The results
for the F_1 diallel cross are presented in Table 7. The
highly significant dam and sire effects demonstrate that the
strain of the parents considerably influenced the level of
performance of the F_1 crosses. The highly significant dam
x sire interaction indicates that the scores of certain
genotypes were statistically different from an expectation
based on an additive gene effects model.

For all the days the effect of sex of offspring is
significant, which indicates that the scores for female and
male mice are significantly different; for days two, three
and the total, the interaction of dams x sex of offspring
is significant. This interaction which is presented in
Figure 3 indicates that the female offspring score much
higher than males when the BALB/cJ strain is the recurrent
dam. The t-test for differences between male and female
offspring over all genotypes in the F_1 diallel cross indicates
that the scores for females are significantly higher in the
number of correct avoidances, except on day one. The results
for the t-tests are presented in Table 8.

DAY 1	Sum of Squares	df	Mean Square	F-ratio
Sires	2493.74	3	831.25	43.31**
Dams	2890.57	3	963.52	50.20**
Sires x dams	2795.35	9	310.59	16.18**
Sex of offspring	128.19	1	128.19	6.68**
Dams x sex	126.64	3	42.21	2.20
Sires x sex	49.02	3	16.34	0.85
Sires x dams x sex	204.11	9	22.68	1.18
Errors	8406.31	438	19.19	

DAY 2				
Sires	2650.11	3	883.37	29.62**
Dams	2900.20	3	966.73	32.41**
Sires x dams	3376.92	9	375.21	12.58**
Sex of offspring	471.82	1	471.82	15.82**
Dams x sex	397.59	3	132.53	4.44**
Sires x sex	460.91	3	15.36	0.51
Sires x dams x sex	252.30	9	28.03	0.94
Errors	13061.1	438	29.82	

DAY 3				
Sires	3016.77	3	1005.59	30.50**
Dams	1355.92	3	451.97	13.71**
Sires x dams	1934.39	9	214.93	6.52**
Sex of offspring	245.40	1	245.40	7.44**
Dams x sex	384.02	3	128.01	3.88**
Sires x sex	167.08	3	55.69	1.69
Sires x dams x sex	282.42	9	31.38	0.95
Errors	1444.24	438	32.98	

TOTAL				
Sires	23263.8	3	7754.59	48.21**
Dams	20148.2	3	6716.07	41.76**
Sires x dams	22464.9	9	2496.10	15.52**
Sex of offspring	2372.56	1	2372.56	14.75**
Dams x sex	2102.06	3	700.68	4.36**
Sires x sex	158.34	3	52.78	0.32
Sires x dams x sex	1417.82	9	157.54	0.98
Errors	70445.4	438	160.83	0.46

** $p < 0.01$

Table 7: Factorial analysis of the F_1 diallel cross.
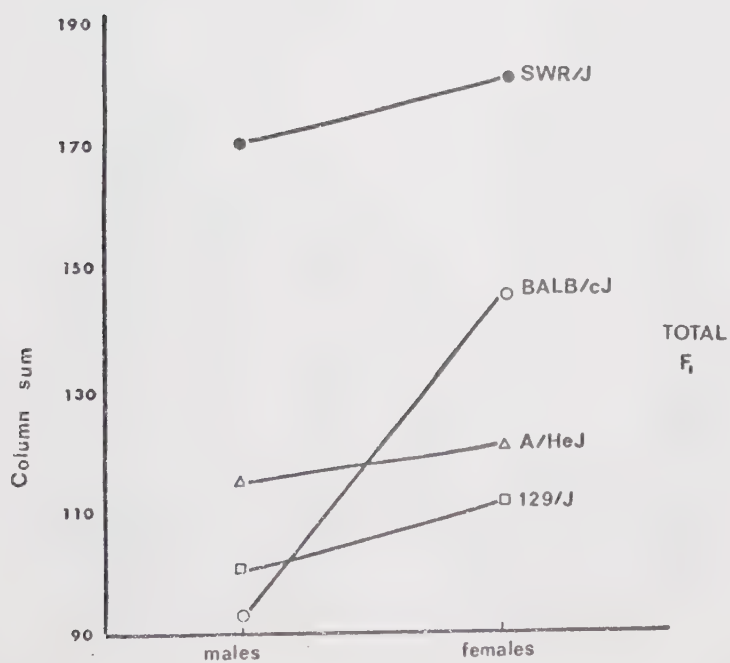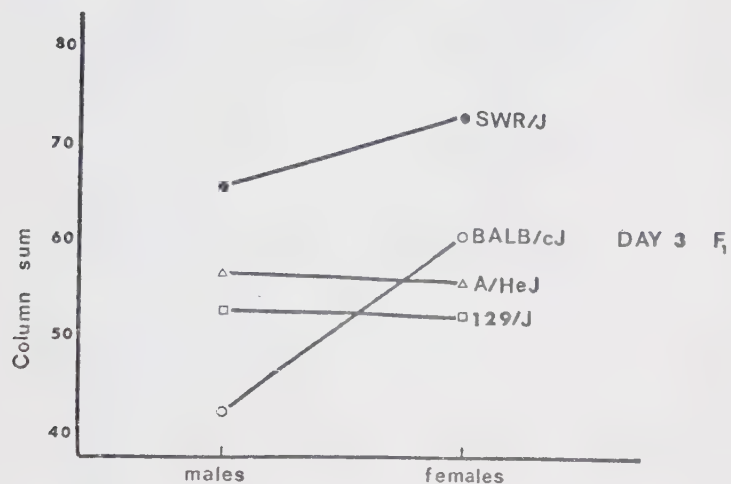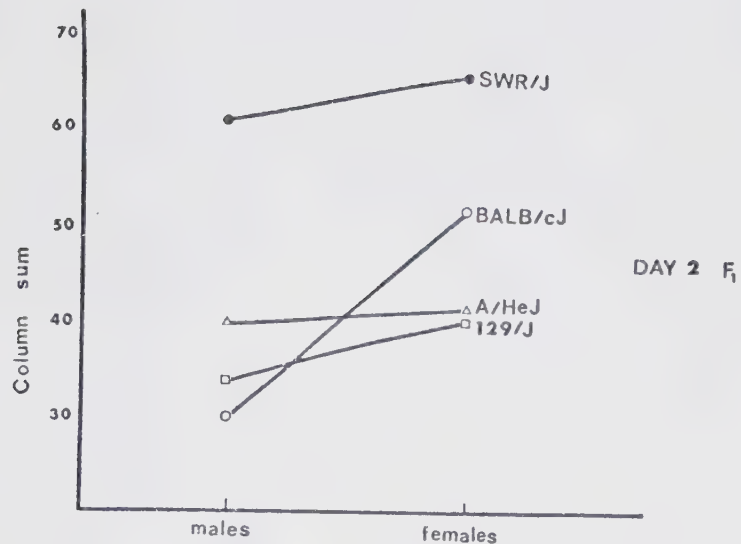
Figure 3: Dam x sex of offspring interaction in F1 diallel.

F_1 DIALLEL CROSS	DAY 1		DAY 2		DAY 3		TOTAL	
	M	F	M	F	M	F	M	F
Mean	6.78	7.63	10.82	12.81	14.13	15.38	31.72	35.81
Standard Deviation	5.86	5.85	6.98	6.62	7.10	6.41	17.53	16.31
t-test	1.59		3.17**		1.98*		2.61**	

N for males = 222
N for females = 248

F_2 DIALLEL CROSS	DAY 1		DAY 2		DAY 3		TOTAL	
	M	F	M	F	M	F	M	F
Mean	8.24	9.19	12.39	13.08	14.14	15.08	34.77	37.35
Standard Deviation	5.97	6.24	6.42	6.47	6.63	6.36	15.79	15.86
t-test	2.64**		1.82*		2.42*		2.75**	

N for males = 554
N for females = 589

** $p < 0.01$
* $p < 0.05$
M = males
F = females

Table 8:   Male versus female scores across all genotypes.

The factorial analysis of the F_2 diallel cross is given in Table 9. The three main effects, that of strain of grandsire, strain of granddam, and sex of offspring, as well as the granddam x grandsire interaction are significant for all days. On day two the interaction between all three main effects is significant. Figure 4 shows that for each set of crosses in which a given strain is the recurrent sire, the relationship between the male and female offspring varies differently. The t-tests for overall differences between males and females, also given in Table 8, over all F_2 genotypes indicates that females score significantly higher in the number of correct avoidances than males for all days. These results are in agreement with those of the F_1 diallel cross except for the three-way interaction on day 2.

In contrast to the F_1 analysis, the granddam x sex of offspring interaction is not significant for any of the days. A reduction in maternal effects in the F_2 would be expected as the distance from the inbred parental strains is further removed by another generation.

DAY 1	Sum of Squares	df	Mean Square	F-ratio
Grandsires (GS)	2303.41	3	767.80	24.98**
Granddams (GD)	2500.73	3	833.58	27.12**
GS x GD	3569.11	9	396.57	12.90**
Sex of offspring	310.80	1	310.80	10.11**
GD x sex	45.47	3	15.16	0.49
GS x sex	118.64	3	39.55	1.29
GS x GD x Sex	320.54	9	35.62	1.16
Errors	39985.9	1301	30.73	

DAY 2				
Grandsires (GS)	2490.80	3	830.27	22.73**
Granddams (GD)	2756.79	3	918.93	25.16**
GS x GD	3033.05	9	337.00	9.23**
Sex of offspring	265.64	1	265.64	7.27**
GD x sex	36.82	3	12.28	0.34
GS x sex	65.82	3	21.94	0.60
GS x GD x sex	762.21	9	84.69	2.31*
Errors	47513.4	1301	36.52	

DAY 3				
Grandsires (GS)	1821.20	3	607.06	15.86**
Granddams (GD)	3080.86	3	1026.95	26.83**
GS x GD	1763.84	9	195.98	5.12**
Sex of offspring	227.97	1	227.97	5.96**
GD x sex	87.70	3	29.23	0.76
GS x sex	121.91	3	40.64	1.06
GS x GD x sex	483.33	9	53.70	1.40
Errors	49790.3	1301	38.27	

TOTAL				
Grandsires (GS)	19369.1	3	6456.37	31.14**
Granddams (GD)	24285.3	3	8095.08	39.04**
GS x GD	22667.1	9	2518.57	12.15**
Sex of offspring	2403.62	1	2403.62	11.59**
GD x sex	432.09	3	144.03	0.69
GS x sex	676.73	3	225.58	1.09
GS x GD x sex	3050.69	9	338.97	1.63
Errors	269747.	1301	207.34	

** $p < 0.01$
* $p < 0.05$

Table 9: Factorial analysis of the F_2 diallel cross.
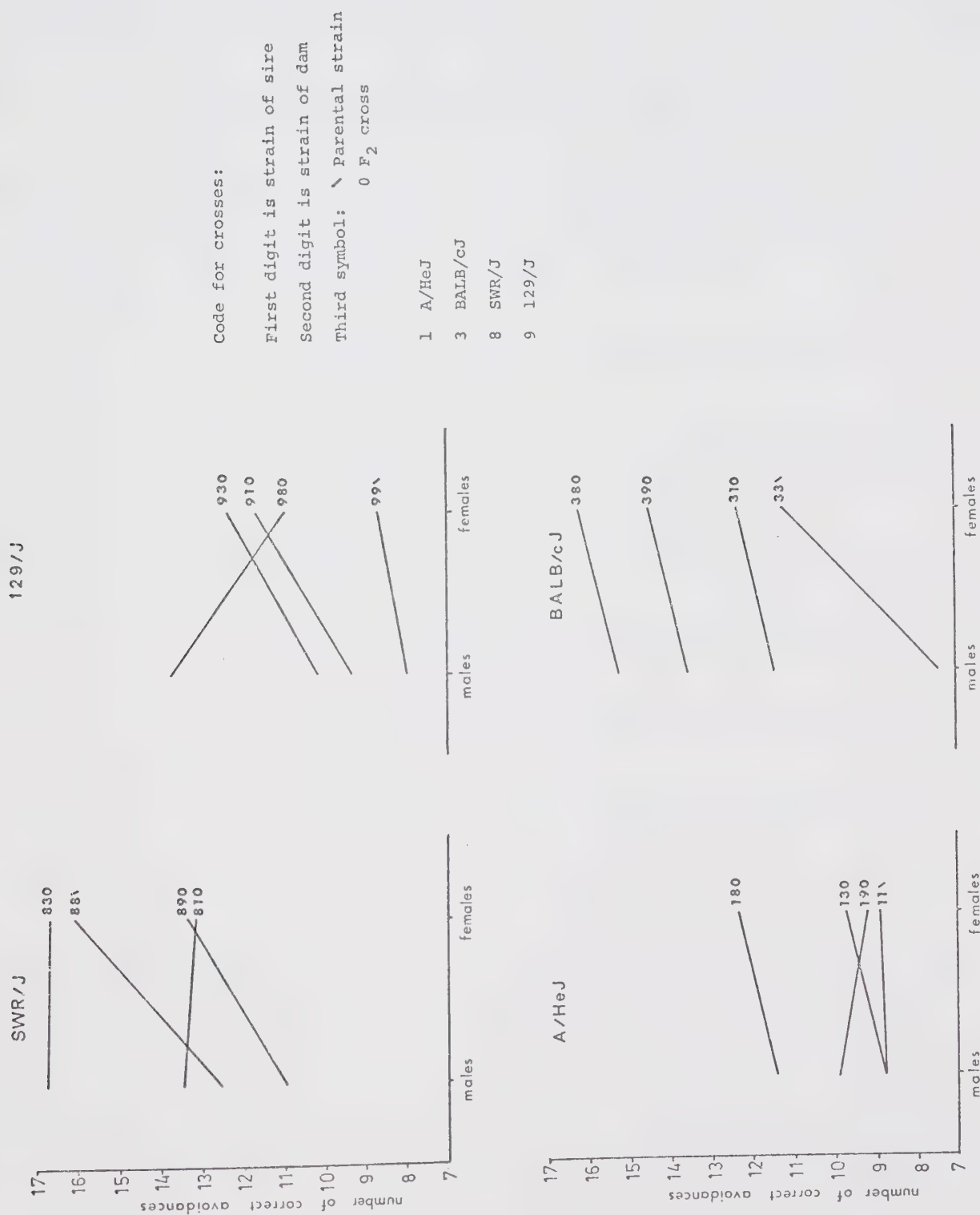
Figure 4: Sire x dam x sex of offspring interaction in F_2 diallel cross on day two.

Hayman's Diallel Cross Analyses

(A)   Analysis of variance of diallel crosses

Hayman's (1954a) analysis of variance of the diallel cross, based on cell means, gives information on the significance of four sources of variance. These are:

(a)   variation between the mean effects of each parental line

(b)   variation in reciprocal sums not ascribable to (a), a measure of dominance which can be subdivided into:

(b_1) mean dominance deviation .

(b_2) further dominance deviation due to the rth parent

(b_3) remaining discrepancy in the rs reciprocal sum

(c)   average maternal effects of each parental line

(d)   variation in the reciprocal differences not ascribable to (c).

In this study (d) is used as the common error as suggested by Hayman (1954a) for non-replicated experiments. Parameters (a) and (b) are respectively analogous to Griffings (1956) general and specific combining ability. Sprague and Tatum (1942) originally defined the term general combining ability "...to designate the average performance of a line in hybrid combination..."; and the term specific combining ability "...to designate thoses cases in which certain combinations

do relatively better or worse than would be expected on the basis of the average performance of the lines involved".

The results are presented in Table 10. For both males and females, item (a), the variation between the mean effects of parental lines is significant or approaches significance at the 0.05 level in both the F_1 and F_2 diallel tables. For the male data, item (b_2) on day one is significant in the F_1 analysis; all measures of dominance variation are significant on day one in the F_2 analysis; and, item (b_1) is significant for the total score in the F_2 analysis. This indicates that for males the parental means are different from the progeny means, that is, there is some overall domin- ance deviation; and, that there is also further dominance deviation due to the rth parent. Item (b_1) for day one is the only significant item due to dominance in the female analysis. In general, the mean squares for the dominance measures are much less in the females.

There are no significant overall maternal effects as measured by item (c) for either sex for any of the days, therefore, the reciprocals were collapsed for the next analysis, Hayman's analysis of diallel crosses.

MALES

Item	df	DAY 1		DAY 2		DAY 3		TOTAL	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
a	3	71.01**	17.96**	72.56*	19.14	49.90*	18.39	573.77*	163.56*
b	6	14.22	10.50***	20.96	8.42	12.77	4.16	133.29	61.64
b_1	1	13.37	35.53**	7.12	31.11	6.09	8.37	77.28	208.26*
b_2	3	21.16*	3.94*	30.04	3.66	10.44	2.26	174.54	23.21
b_3	2	4.25	7.84*	14.25	4.23	19.60	4.92	99.41	45.97
c	3	1.98	0.58	13.19	1.13	26.75	2.28	68.15	10.88
d	3	1.94	0.36	6.43	4.09	3.23	2.35	28.31	13.71

FEMALES

Item	df	DAY 1		DAY 2		DAY 3		TOTAL	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
a	3	64.62*	23.51**	63.61*	23.47	42.99	22.38	494.21*	196.97
b	6	11.77	8.27	8.73	4.09	6.22	3.31	67.36	39.44
b_1	1	9.01	26.80**	8.67	9.58	12.12	5.90	88.88	114.53
b_2	3	15.13	2.96	9.70	0.72	4.96	0.93	80.49	4.27
b_3	2	8.12	6.96	7.32	6.40	5.16	5.58	36.90	54.64
c	3	1.60	0.93	0.45	1.19	4.40	0.88	3.38	8.55
d	3	4.04	2.25	6.62	4.27	6.03	2.44	31.47	24.66

Table 10: Mean squares for Hayman's analysis of variance.

** $p < 0.01$

* $p < 0.05$

(B)   Analysis of diallel crosses

Hayman's (1954b) analysis of diallel crosses was performed on the data using Aksel & Johnson's (1963) worked example to estimate the size of several genetic parameters and ratios derived from these estimates.   The results are presented in Tables 11 and 12 and also in Figures 5 and 6. Assumptions that are made for this analysis are:

> (1)   diploid segregation,
>
> (2)   no reciprocal differences,
>
> (3)   independent action of non-allelic genes;
>
> and in the diallel cross:
>
> (4)   no multiple allelism,
>
> (5)   homozygous parents,
>
> (6)   genes independently distributed between the parents.

The validity of the hypotheses postulated is tested by Hayman's (1954b) t-test for the case when the experiment is not replicated.   The appropriate formula is:

$$t^2 = \frac{n-2}{4} \times \frac{(\text{var } V_r - \text{var } W_r)^2}{(\text{var } V_r \times \text{var } W_r) - \text{cov}^2 (V_r, W_r)}$$

where   var = variance

cov = covariance

V_r = variance of the rth array

W_r = covariance of the rth array with the pure strains

with n-2 degrees of freedom where n = the number of parental strains.   Significance of the t-test indicates that W_r - V_r,

	DAY 1		DAY 2		DAY 3		TOTAL	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
D	6.75± 4.81	8.23±2.01*	-4.31± 6.47	2.89±1.76	-6.53± 4.14	6.14±1.10**	18.90± 43.87	54.84±14.37*
H_1	34.13±13.98*	21.80±5.84*	32.40±18.82	12.15±5.12	-6.72±12.04	3.66±3.19	233.28±127.52	104.16±41.76*
H_2	24.53±12.91	20.07±5.39*	22.29±17.37	11.63±4.73	-4.45±11.12	3.70±2.95	170.13±117.71	98.71±38.55*
h	8.56± 8.76	26.29±3.66**	-2.02±11.78	21.38±3.20**	-6.68± 7.54	4.54±2.00	21.79± 79.84	146.98±26.15**
F	-18.18±12.36	1.23±5.16	-25.56±16.63	-4.85±4.52	-26.26±10.64	-1.92±2.82	-180.70±112.70	-15.33±36.91
E	1.96± 2.15	0.47±0.90	9.81± 2.90*	2.61±0.79*	14.99± 1.85**	2.32±0.49*	48.23±119.62*	12.29± 6.42
$(H_1/D)^½$	2.25	3.25	–	4.10	–	1.54	3.51	2.75
$H_2/4H_1$	0.18	0.23	–	0.24	–	0.25	0.18	0.24
$\dfrac{(4DH_1)^½ + F}{(4DH_1)^½ - F}$	0.25	1.10	–	0.42	–	0.66	-0.15	0.86
$\dfrac{\text{Additive var}}{\text{Total var}}$	0.16	0.08	–	0.05	–	0.26	0.06	0.11
Hayman's t-test	0.53	0.00	2.36	0.03	2.21	0.01	1.15	0.01
b coefficient	0.64± 0.29	0.86±0.34	0.47± 0.22	0.82±0.32	0.58± 0.20	0.88±0.29	0.58± 0.25	0.85± 0.32
t-test (1-b)	1.24	0.42	2.39	0.55	2.13	0.42	1.68	0.46
Intercept	-1.85	-2.49	-2.57	-2.11	-0.29	0.28	-13.67	-9.39

** p < 0.01
* p < 0.05

Table 11: Results from Hayman's analysis of diallel crosses for MALES.

	DAY 1		DAY 2		DAY 3		TOTAL	
	F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
D	5.93± 5.10	7.15±1.97*	8.40±2.40*	9.20±0.71**	8.94±2.38*	12.51±0.87**	75.24±20.81*	76.06± 4.26**
H_1	24.06±14.84	14.03±5.22*	13.48±6.98	1.71±2.07	1.83±6.93	2.93±2.52	131.40±60.49	39.50±12.38*
H_2	17.91±13.70	13.35±4.82*	10.40±6.44	2.72±1.92	1.97±6.40	3.30±2.33	99.87±55.84	45.67±11.43*
h	4.64± 9.29	18.90±3.26**	3.85±4.37	5.14±1.30*	5.17±4.34	3.18±1.58	53.59±37.87	73.45± 7.75**
F	-18.82±13.12	-3.12±4.61	-18.56±6.17*	-2.17±1.83	-10.08±6.12	1.78±2.23	-131.61±53.46*	-20.28±10.94
E	2.82± 2.28	1.59±0.80	3.53±1.07*	2.73±0.32*	5.24±1.07*	1.66±0.39*	17.43± 9.31	16.60± 1.90**
$(H_1/D)^{\frac{1}{2}}$	2.01	2.80	1.27	0.86	0.45	0.97	1.32	1.44
$H_2/4H_1$	0.19	0.24	0.19	0.40	0.27	0.28	0.19	0.29
$\dfrac{(4DH_1)^{\frac{1}{2}} + F}{(4DH_1)^{\frac{1}{2}} - F}$	0.12	0.73	0.14	0.57	-0.11	1.34	0.20	0.62
$\dfrac{\text{Additive var}}{\text{Total var}}$	0.18	0.11	0.33	0.50	0.56	0.48	0.34	0.30
Hayman's t-test	1.89	0.26	0.44	2.04	0.06	0.00	0.16	4.29
b coefficient	0.48± 0.24	0.37±0.45	0.75±0.24	1.36±0.43	0.84±0.28	0.97±0.17	0.78± 0.29	1.24± 0.14
t-test (1-b)	2.19	1.40	1.03	-0.84	0.56	0.15	0.78	-1.72
Intercept	1.75	2.11	0.45	-0.97	1.14	1.89	0.72	-7.70

** p < 0.01
* p < 0.05

Table 12: Results from Hayman's analysis of diallel crosses for FEMALES.

is not constant and the assumptions are not met. Hayman
(1954b) states that the weakness of this test is that it only
detects variation in $W_r - V_r$ which is correlated with the
dominance order of the parents. Variation which merely
increases the scatter of points about the regression line of
W_r on V_r without altering its slope can not be detected by
this test. This latter variation can only be detected by
analyzing line and block differences when the experiment is
replicated. Also if $W_r - V_r$ is constant, the V_r, W_r graph
should be a straight line of unit slope. The t-tests for
the present data were not significant for either sex for
any of the days.

The following components of variation were estimated:

D, variation due to additive effects of genes;

H_1, variation due to dominance effects of genes;

H_2, variation due to dominance effects indicating
asymmetry of positive and negative effects
of genes;

h, variation due to dominance effects as the sum
over all loci in the heterozygous phase in
all crosses;

F, covariation of additive and dominance effects;

E, variation due to environmental effects.

The components of variation were used to provide estimates
of the following ratios:

$$(H_1/D)^{\frac{1}{2}} = \text{mean degree of dominance}$$

$$H_2/4H_1 = \text{the proportion of genes with positive}$$
and negative effects in the parents;

$$(4DH_1)^{\frac{1}{2}} +F/(4DH_1)^{\frac{1}{2}}-F = \text{the ratio of the total number of domin-}$$
ant to recessive genes in the parents;

$$D/(D + H_1 + E) = \text{additive var/ total var} = \text{heritability.}$$

The estimates of D, H_1 and E are compared in Figures
5 and 6 for both the F_1 and F_2 diallel crosses for each sex.
Johnson & Aksel (1959) have demonstrated that Hayman's (1954a,
1954b) formulae can be used with one consideration for any
generation. That is, for the nth filial generation, (fn),
$H_1=((\frac{1}{2})^{fn-1} h)^2$ and, in particular, for the F_2, H_1 has a value
one-fourth that in the F_1. Except for days two and three for
males the results of this analysis show that the estimates of
D are about equal in the F_1 and F_2 diallel crosses as would
be expected, but H_1 in the F_2 is larger than expected in
comparison to the estimate in the F_1 diallel cross. This
latter result may mean that dominance is being suppressed in
the F_1 or the estimate may be distorted due to the high degree
of asymmetry of positive and negative effects in the parents
as measured by the ratio $H_2/4H_1$, and confirmed by the ratio
of dominant to recessive gene effects in the parents which
are more unequal in the F_1 diallel cross. Heritability
estimates which are also given in the graphs are much higher
for females.

Figure 6: Genetic parameters for females. (Heritability estimates are shown above the bar graphs.)

Figure 5: Genetic parameters for males.

In the male F_1 data the variation due to error increases until by day three it accounts for all the variation. This accounts for the negative values of D and H_1 (Table 11) obtained for days two and three which do not have a valid interpretation. This is evidenced by the increased reciprocal differences and by the low regression coefficients which deviate further from unity in the males than in the females.

Although only a few of the estimates are significant, the results are consistent with the results of Hayman's analysis of variance. In both analyses the significance of both additive and dominance components decreased over days, and variation due to dominance effects are less in the females.

In the F_2 analysis significance of h, except on day three, indicates significant variation due to dominance effects as the algebraic sum over all loci in the heterozygous phase in all crosses.

Estimates of $(H_1/D)^{\frac{1}{2}}$ which measure the mean degree of dominance are also given in Tables 11 and 12. If complete dominance is exhibited, the ratio is 1.0; overdominance is indicated by a ratio of greater than 1.0 and partial dominance by a ratio of less than 1.0. The ratio is consistently higher for males than females, and in the males is always greater than 1.0, whereas in the females three of the eight estimates are less than 1.0.

(C) Variance-covariance graphs

Variance-covariance diagrams were plotted for each sex for the three consecutive days of testing and for the mean total of correct avoidances. These are presented in Figures 7 and 8. The variance of the rth array, V_r, forms the abscissa; and the covariance, W_r, of the rth array with the pure strains forms the ordinate.

An overall assessment of the degree of dominance is obtained from the V_r, W_r graph. If complete dominance is exhibited the regression line of covariance on variance passes through the origin; overdominance is indicated by an intercept below the origin and partial dominance by an intercept above the origin. Males tend toward slight over-dominance and females tend toward partial dominance. This agrees with the estimates of $(H_1/D)^{\frac{1}{2}}$.

The spacing of the V_r, W_r points along the regression line enclosed by the limiting parabola, $W_r^2 = V_r \times V_{OLO}$, where V_{OLO} is the variance of the parents, shows the relative proportion of dominant and recessive genes in each strain. Points close to the origin represent strains possessing mainly dominant genes, whereas, points farthest from the origin represent strains possessing mainly recessive genes.
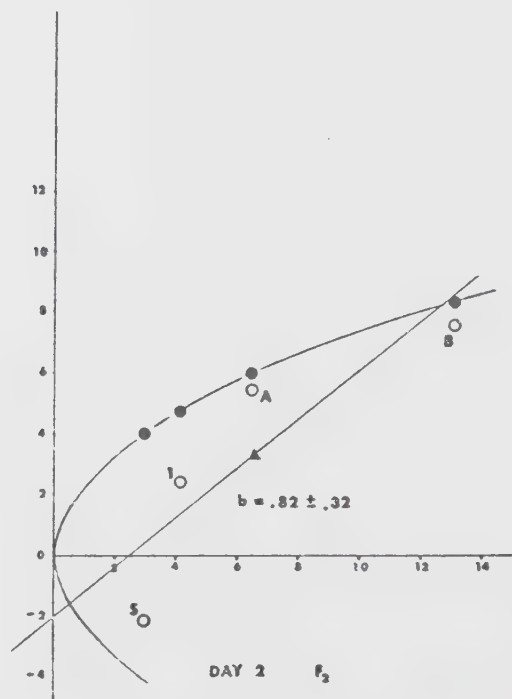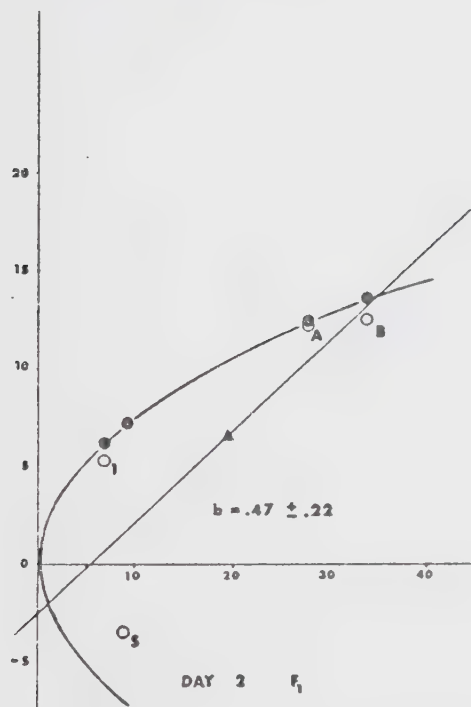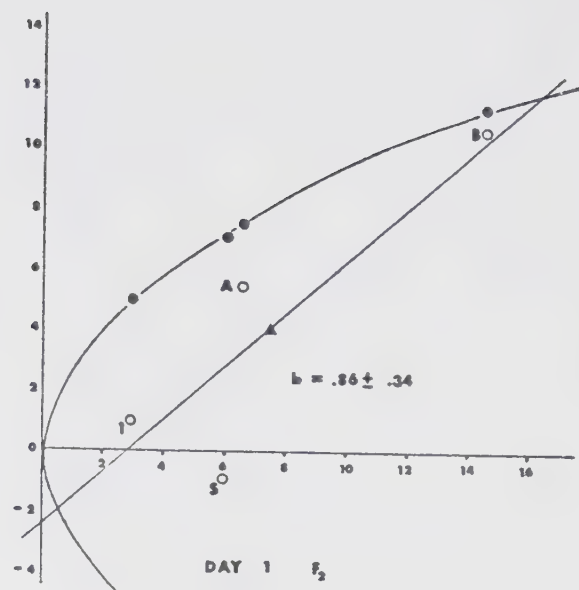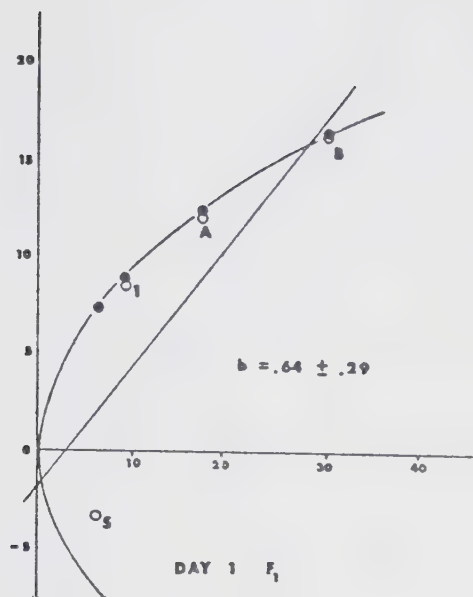
A	A/HeJ	x-axis	Vr		$\circ$	V_r, W_r
B	BALB/cJ	y-axis	Wr			
S	SWR/J	$\blacktriangle$	$\overline{V}, \overline{W}$		$\bullet$	$\sqrt{V_r, V_{OLO}}$
l	129/J					

Figure 7:   Vr,Wr graphs for males for day one and two.
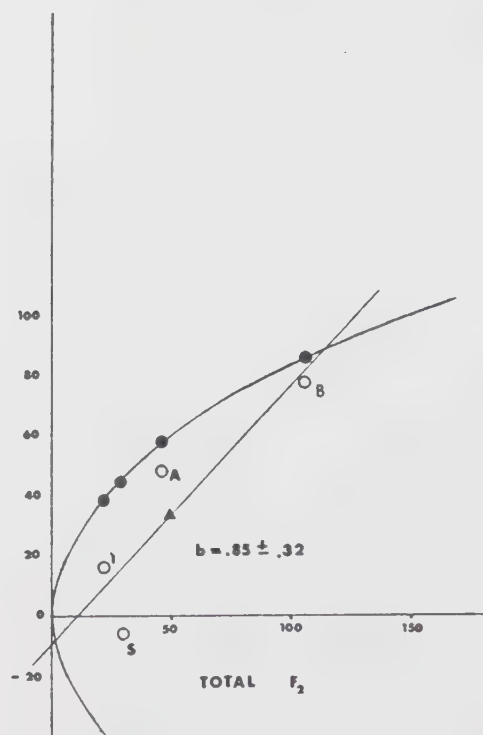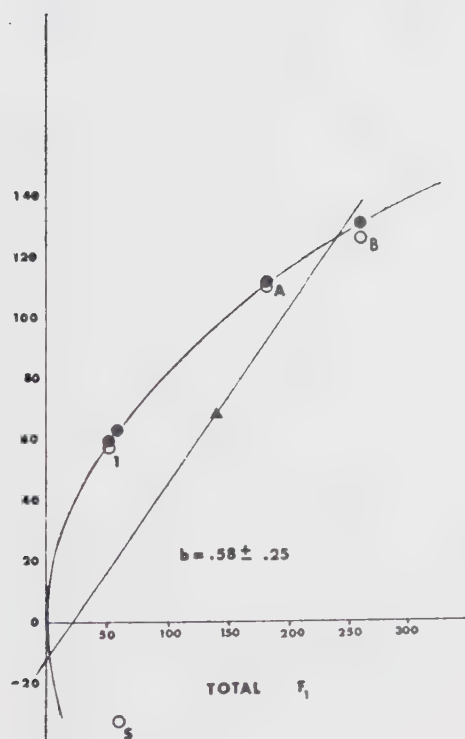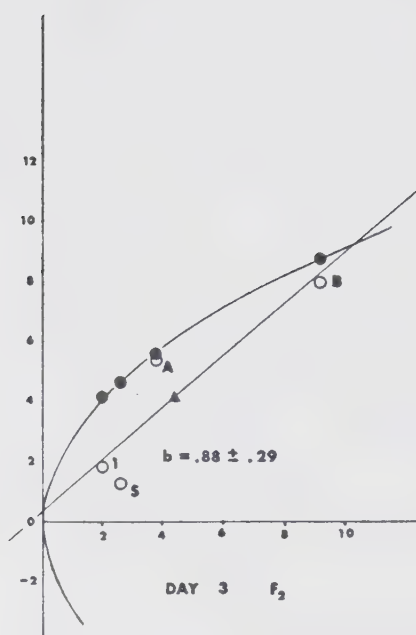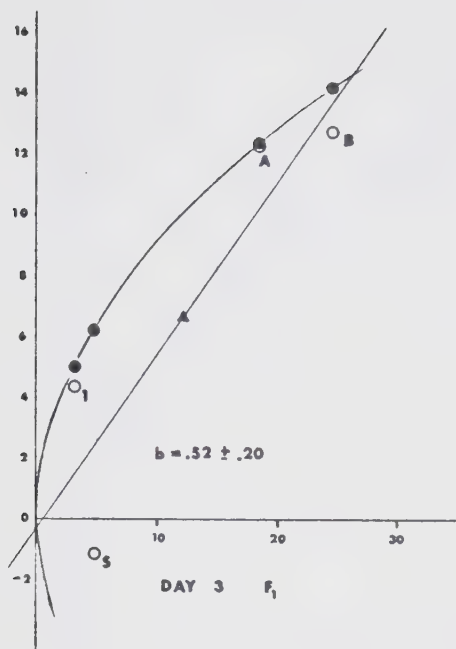
Figure 7 cont'd: Vr,Wr graphs for males for day three and total.
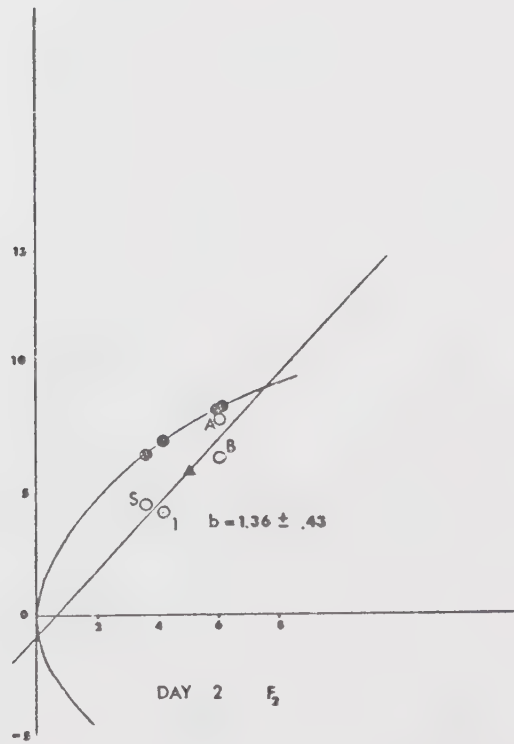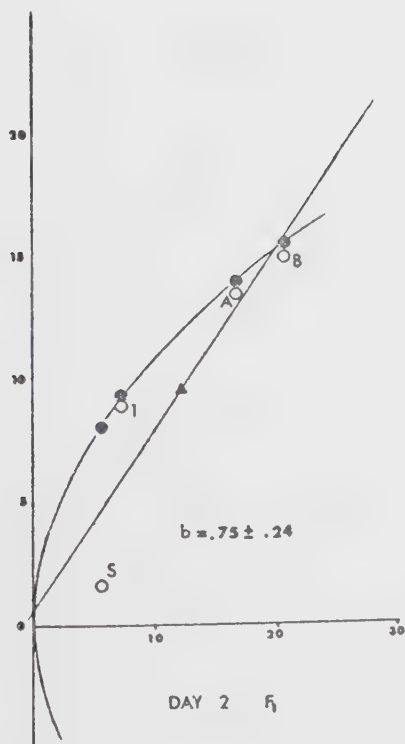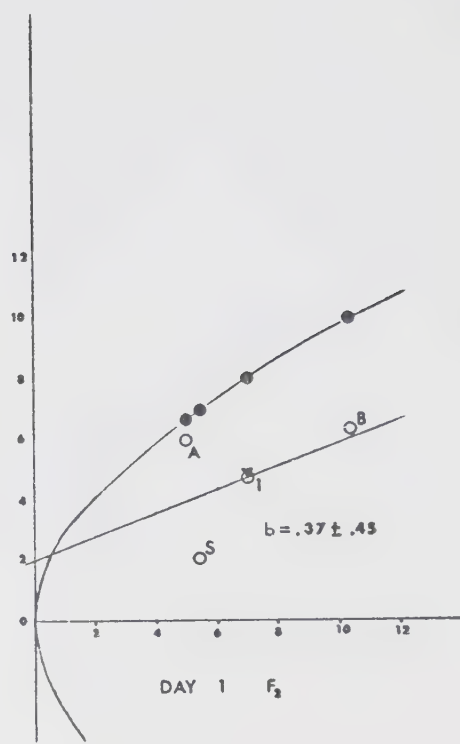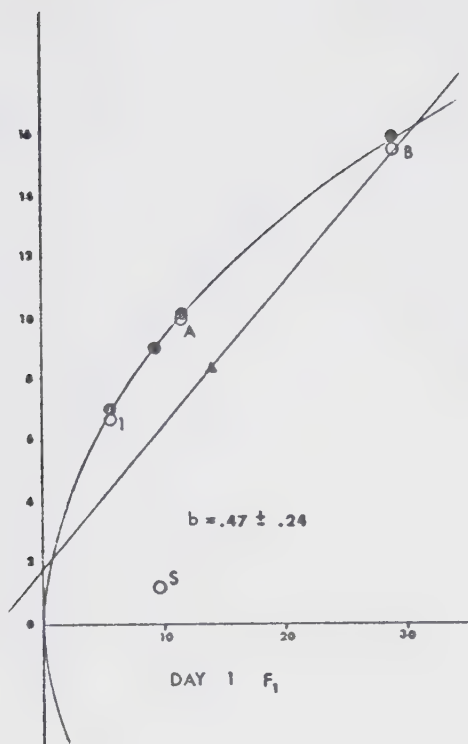
Figure 8: Vr,Wr graphs for females on day one and two.
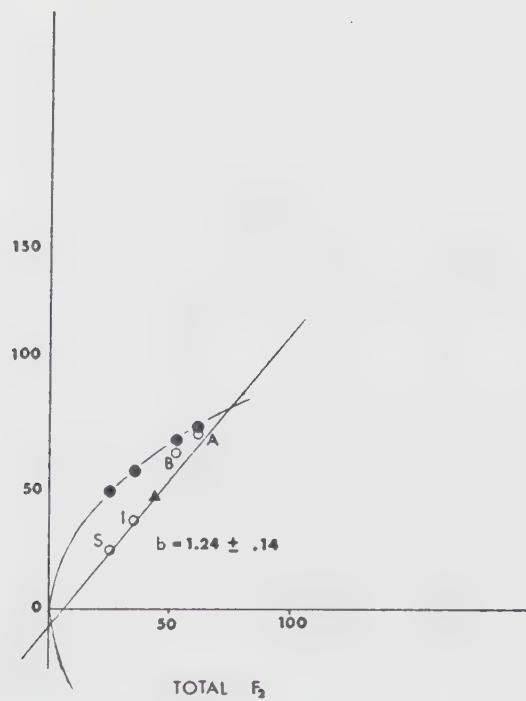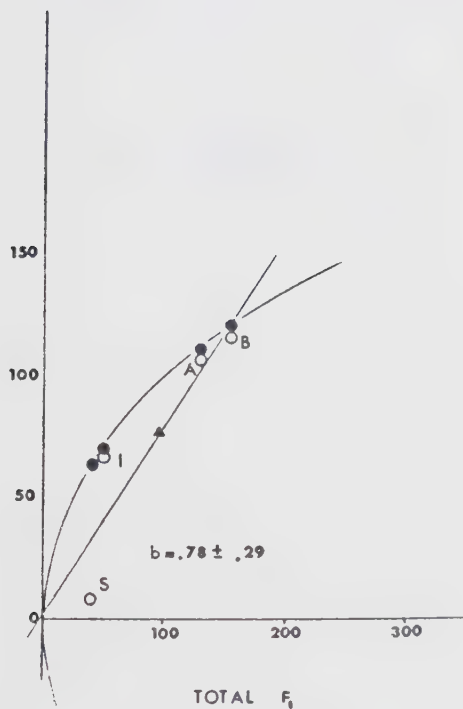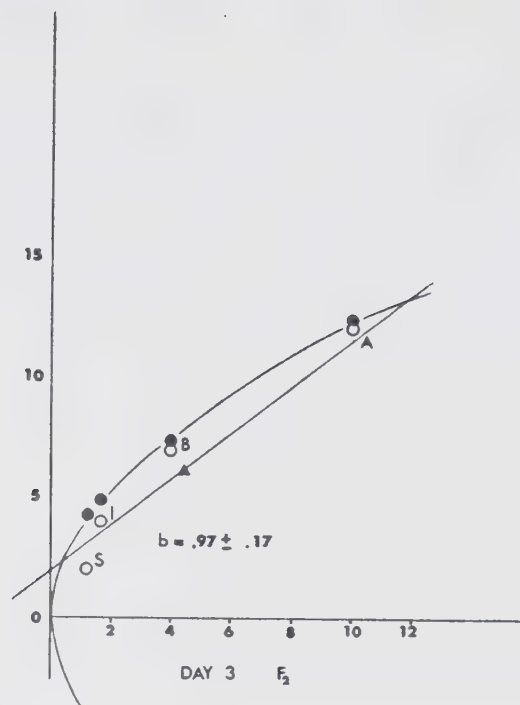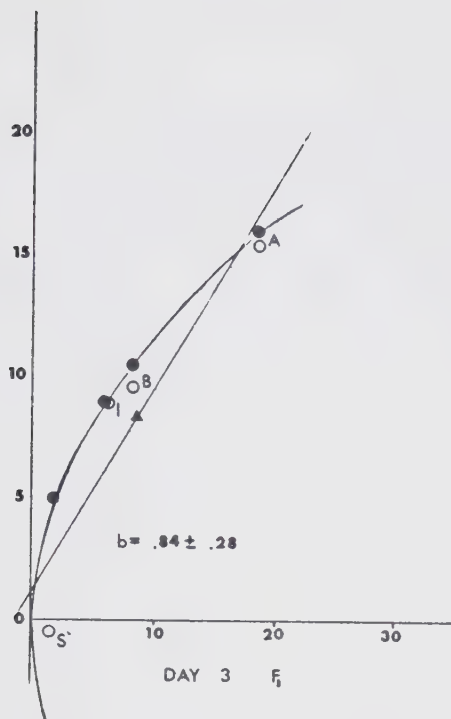
Figure 8 cont'd: Vr,Wr graphs for females for day three and
total.

The points are spaced out along the regression line, but there are too few points to come to a definite conclusion. The rank ordering of strains is similar for both sexes, however, the SWR/J strain is highly overdominant in the males, that is, it is located far below the x-axis, and in the females it is partially dominant being located above the x-axis except on day three when it is slightly below the x-axis. This difference accounts for the overall overdominance in the males and the reduced overall degree of dominance found in the females.

Classical Analysis

This analysis, first developed by Mather (1949), starts with two inbred strains, P_1 and P_2, which are crossed to produce the first filial generation, F_1. The F_1 is crossed inter se to produce the second filial generation, F_2; and is also crossed with each parental strain to produce the backcross generations designated as B_1 and B_2. This analysis, which has never been applied to a measure of learning (Wahlsten, 1971), is based on two assumptions: (1) That genetic interaction between loci is absent, and (2) that genotype-environment interaction is absent.

The first assumption is tested by a method developed by Cavalli-Sforza (1952) which consists of

estimating by a weighted least-squares approach, the three parameters, m, d, and h, which are respectively the mean, additive, and dominance components of the generation means. The weights used are the reciprocals of the squared standard errors of the mean of each genetic group. The deviations between the expected means derived on the basis of the genetic model using the estimates of the parameters and the observed mean for each genetic group is squared and weighted. The sum, over groups, of these deviations is distributed as a chi-square with degrees of freedom equal to the number of groups utilized minus the number of parameters estimated.

The second assumption is tested by comparing the variances of the three non-segregating groups.

The following values are estimated:

V_e, environmental variance;

V_d, additive variance;

V_h, variance due to dominance effects;

h^2, heritability in the narrow sense;

$(V_h/V_d)^{\frac{1}{2}}$, dominance ratio;

(V_t/V_e), F_{max} test for segregation.

Over one-half of the chi-squares are significant especially on day one, and 27 percent of the F_{max} ratios are significant. This indicates violation of the two assumptions, the presence of non-allelic and genotype-environment interaction, for many of the sets.

The results of this analysis are graphically presented in Figures 9 and 10 and are given in Appendix III. The results seem to fall into two main categories. The first category involves those crosses in which SWR/J is a parental strain. In crosses with A/HeJ and BALB/cJ, the F_1 show strong overdominance. All three parameters, m, d, and h are significant. In its cross with 129/J, the F_1 is partially dominant in the direction of SWR/J, and only m and d are significant.

The second category involves the strains, A/HeJ, BALB/cJ and 129/J which have similar means. In the A/HeJ x BALB/cJ and A/HeJ x 129/J crosses the F_1 averages below the lower scoring parent except on day three. In the BALB/cJ x 129/J cross the F_1 score similarly to the parental strains. In all three of these crosses the F_2 and backcross score much higher than expected.

As far as estimates from the second-degree statistics, less than one-quarter have estimates of the variances that are interpretable. In the rest of the sets of data, negative estimates which do not have a valid interpretation are obtained.

Figure 9: Relationship among the segregating and non-segregating generation means.
(Crosses involving SWR/J)
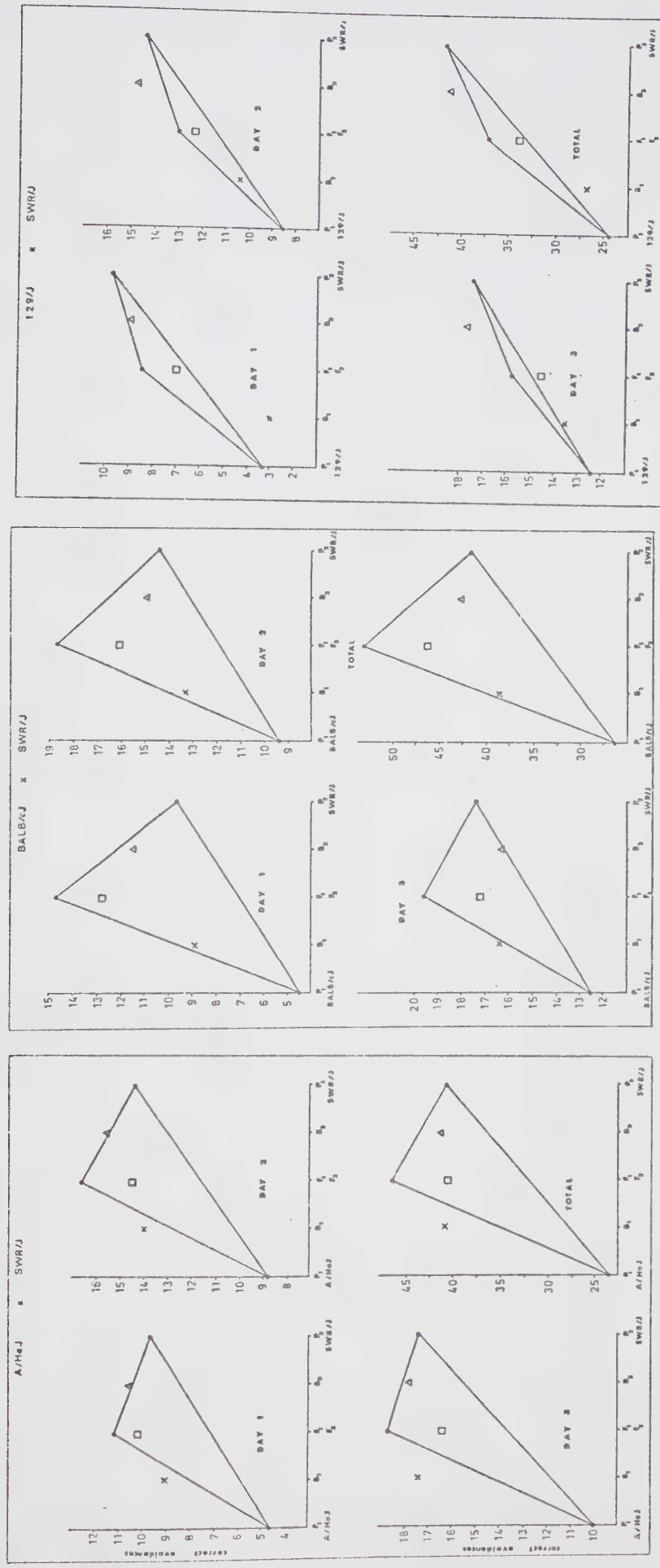
● non-segregating generations means (P_1, P_2, F_1)
□ F_2 mean
✕ mean of backcross to P_1
△ mean of backcross to P_2
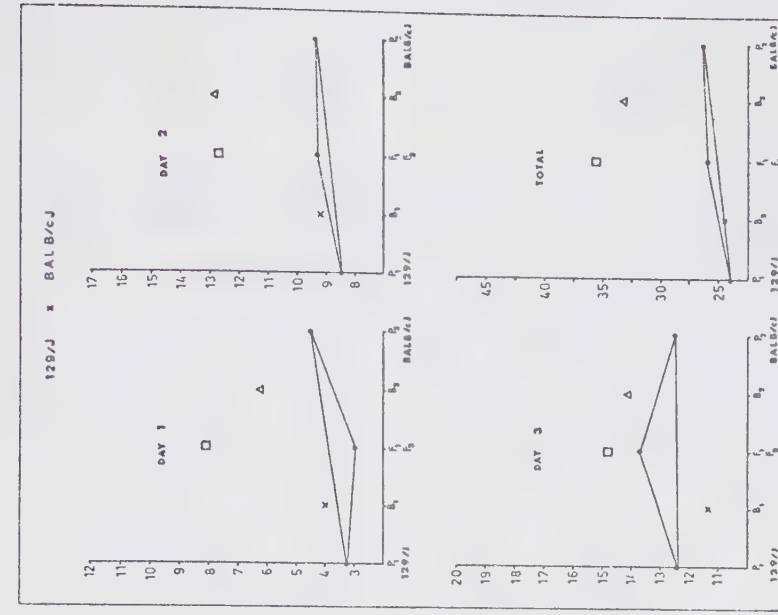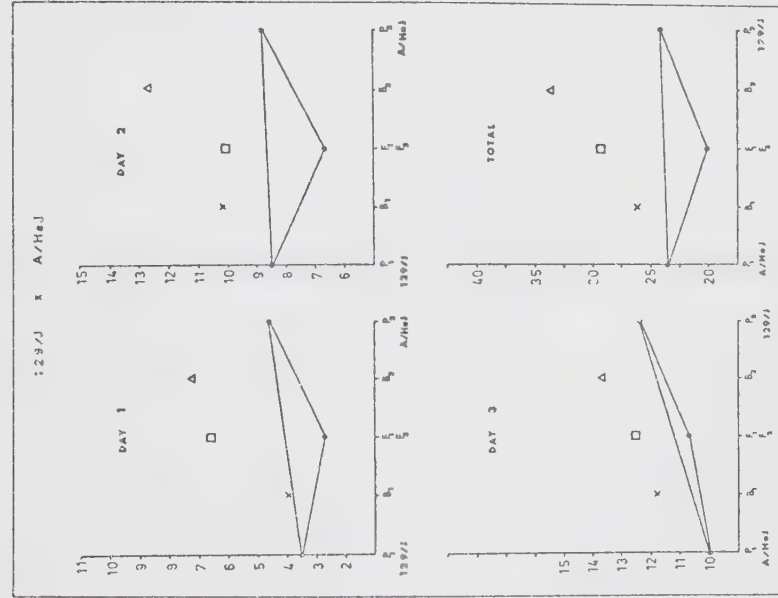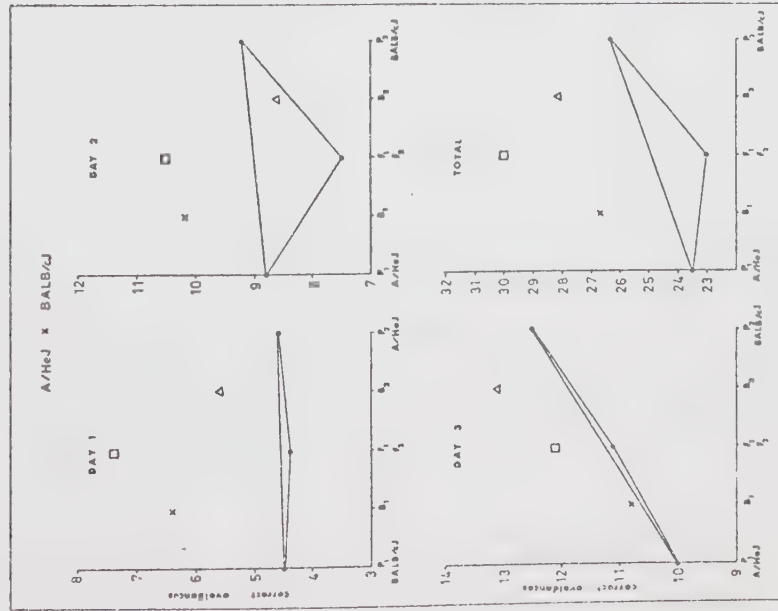
non-segregating generations mean (P_1, P_2, F_1)

F₂ mean

mean of backcross to P_1

mean of backcross to P_2

Figure 10: Relationship among the segregating and non-segregating generation means.
(Crosses involving A/HeJ, BALB/cJ and 129/J)

The problem stems mainly from the high estimates of variance due to the environment. The presence of negative variances prohibits the calculation of further ratios. Using the F-ratio of total variance to environmental variance, significant genetic variation in avoidance behavior in the F_2 generation is shown only for day one. Other reasons for failure to show significant genetic variation will be considered in the discussion section.

Square root transformation was applied and analysis was carried out with no improvement. V_d and V_h negative estimates persisted where present in the analysis of the raw data given above. The raw data was also analyzed with the data restructured with the sexes separate and the reciprocals collapsed and also with the sexes collapsed and the reciprocals separate to provide 12 equations. The chi-squares from these analyses were all significant except one. The analysis of the sexes separately with the reciprocals combined into six equations improved four of the sets and are given in the appropriate places in Appendix III.

The dominance ratio, $(V_h/V_d)^{\frac{1}{2}}$, when calculated where possible, indicates overdominance. The estimates of heritability are low. These results are in agreement with the previous analyses.

Relationship of Avoidance Behavior with Other Variables

For the F_1 and F_2 diallel crosses and the back-
crosses, a matrix of correlations of ten variables is
presented in Appendix IV. The variables are: weight on the
first day of testing; litter size; the number of correct
avoidances on days one, two and three; the number of cross-
ings of the midline during intertrial intervals for days
one, two and three; and age of sires and dams on day of
birth. In each of the matrices the numbers of correct
avoidances and the numbers of crossings over the midline
are highly intercorrelated. That is, the more active the
animal was, the more correct responses it made. Litter size
is positively correlated with the number of correct avoid-
ances on day one in both the F_1 diallel cross and in the
backcrosses, but not in the F_2 diallel cross. In only the
F_1 diallel cross, weight is negatively correlated with
avoidance behavior on all days. In the F_2 diallel cross
the ages of the sires and dams are correlated with all
other variables, whereas, in the backcrosses the age of the
sires is not significantly correlated with any of the
variables and age of the dam is correlated with half the
variables. Only a few variables are significantly
correlated with the ages of the sires and dams in the F_1
diallel cross.

Although the number of correct avoidances is correlated with weight, litter size, and the ages of the sires and dams, the correlations are not consistent in the three sets of data nor are they very strong correlations.

DISCUSSION

The levels of avoidance behavior evident in the inbred strains are similar to those already reported by Royce, et al (1971) and Royce (1972) with the exception of the A/HeJ strain. The A/HeJ strain and all its F_1 crosses score much lower in the present study. The F_1 diallel cross correlates with the corresponding subset of the Royce, et al (1971) diallel cross 0.69 ($p<0.005$) for males and 0.50 ($p<0.025$) for females. The overall mean of the diallel cross in the present study is lower, (30.2 vs 47.0 for males; 35.0 vs 49.1 for females); but, the overall standard deviation is higher, (13.3 vs 8.5 for males; 11.2 vs 8.1 for females). The only obvious difference that may account for the decrease in the mean level of performance especially for A/HeJ and its crosses, and the increase in differentiation between genotypes is the change in the conditioned stimulus from a buzzer to a tone.

The presence of significant overall sex differences for the F_1 diallel as indicated by the factorial analysis (Table 7) and the t-tests (Table 8) agrees with Royce, et al (1971) and Collins (1964). In all three studies females are superior to the males in avoidance behavior. Oliverio, et al (1972) did not find any significant sex difference. There were no strains in common with the present study, but two of the three strains used by Oliverio, et al (1972) were in

common with the Collins' (1964) study. It may be that the
apparatus and procedure used by Oliverio, et al (1972) does
not produce differentiation between the sexes.

There is no overall maternal effect in either the
F_1 or F_2 diallel table as measured by the "c" term in
Hayman's analysis of variance of the means (Table 10); but,
there is a specific maternal effect on days two and three
for the F_1 diallel table such that when the BALB/cJ strain is
the recurrent dam, female offspring score much higher than
male offspring.

Hayman's (1954a) analysis of variance (Table 10)
gives an overall assessment of hereditary influences and type
of gene action. The variation due to additive gene effects
or general combining ability is significant and agrees with
that of Collins (1964) and Oliverio, et al (1972); but, the
present study disagrees with these studies in that specific
combining ability is not significant except for day one in
males. Variation due to dominance effects or specific
combining ability may not be significant in the present
study because of a cancelling out of the dominance effects
in that dominance towards increasing the score is balanced
by dominance towards decreasing the score. This is supported
by the results of the classical analysis (Figures 7 and 8 and
Appendix III) in which two of the six crosses exhibit over-
dominance toward the high scoring parent, two to the low

scoring parent, and two exhibit partial dominance.

The overall mode of inheritance is overdominance with the effect more pronounced in males than in the females. Other studies which report an overall overdominant mode of inheritance are Collins (1964), van Abeelen (1966), Schlesinger & Wimer (1967), Henderson (1968), and Parsons & Rose (1970). Royce, et al (1971) and Oliverio, et al (1972) report complete dominance. From the present study, and that of Royce, et al (1971) and Collins (1964), it can be seen that in individual crosses various modes of inheritance are displayed. The mean dominance ratio, $(H_1/D)^{\frac{1}{2}}$, indicates strong overdominance for males, whereas, for females all modes of inheritance, overdominance, complete dominance and partial dominance, are displayed. This difference in expression is evidenced in that the variation due to dominance effects, H_1, is consistently larger in males than females. In addition, D, the component of variation due to additive effects is less in the females. This is also shown in the variance-covariance graphs in which the regression line passes further below the y-axis in the males than females. This relationship of greater estimates of H_1 in males and greater estimates of D in females accounts for the much higher estimates of heritability in the females. Table 13 presents a comparison of the dominance ratio and heritability estimates between the present study and those studies in which the data was reported.

	MALES				FEMALES			
Day	1	2	3	Total	1	2	3	Total
Present Study F_1	0.16	-	-	0.06	0.18	0.33	0.56	0.34
F_2	0.08	0.05	0.26	0.11	0.11	0.50	0.48	0.30
Royce, et al (1971) F_1	0.52	0.50	0.35	0.50	0.52	0.38	0.56	0.50

Oliverio, (1971)   0.50 by intrasire regression of F_3 offspring on F_2 dams and correlation between sibs.

	MALES				FEMALES			
Day	1	2	3	Total	1	2	3	Total
Present Study F_1	2.25	-	-	3.52	2.02	1.27	0.45	1.32
F_2	3.25	4.10	1.54	2.75	2.80	0.86	0.97	1.41
Royce, et al (1971) F_1	0.81	0.93	1.32	0.93	0.90	1.15	0.80	0.96

Oliverio, et al (1972)   1.00

Table 13: Comparison of results with those of Royce, et al (1971) and Oliverio, et al (1972). (Upper table shows heritability estimates; lower table shows mean degree of dominance.)

The present results do not seem to be in consistent agreement with the estimates by Royce, et al (1971) nor do the same relationships hold between males and females. Oliverio, et al (1971), using a randomly bred strain, CD1, and an inbred strain, SEC/1ReJ, estimated heritability by full- and half-sib correlations and by intrasire regression of offspring on dams to be about 0.50. Oliverio's (1971,1972) estimates of both the dominance ratio and heritability are in agreement with those of Royce, et al (1971).

At this time it does not seem meaningful to relate these results into an evolutionary framework except at a superficial level. It is readily believable that avoidance behavior may be of greater adaptive significance to females whose safety is directly related to the survival of the offspring and this is reflected in the higher number of correct avoidances obtained by females. If this is the case we would expect that a stronger selection pressure for high avoidance behavior in females would have taken place. If it had, we would expect lower heritabilities in females because had selection been operating the variation due to additive effects would be diminished. This was not found in the present study; that is, more variation due to additive effects was found in females than males. It also may be that this measurement is only tangentially related to avoidance behavior in the mouse's natural environment.

We would not expect avoidance behavior to be under rigid genetic control as a fixed behavioral response would not be adaptive, but rather a general behavior pattern which would be fitted to individual situations would probably be inherited.

To date avoidance behavior has not been analyzed using the classical method. This method provides the best assessment of epistatic gene action and potentially provides a great deal of specific genetic information. The graphs (Figures 7 and 8) from the classical analysis of the six group means further illustrates the various dominance relationships in individual crosses. This analysis is useful in pointing out the differences in the crosses involving SWR/J but not in the other cases. The lack of significance of h, the component of the group means due to dominance effects, in the crosses not involving SWR/J means either that dominance is absent or if there is dominance at individual loci, the effects are in opposition (Appendix III). The components of variance estimated from the second-degree statistics are not in general meaningful. The occurrence of negative values when applying biometric genetic formulas is not unusual (Wright, 1952; Newell, 1970). The problem obtains mainly from the variance due to environmental effects which is large. The presence of genotype-environment interaction is another serious problem because its effects on estimates of genetic parameters are

unknown. There is nothing in the theoretical framework of quantitative genetics to indicate the magnitude of the effects produced when this assumption is violated. Both Newell (1970) and Broadhurst & Jinks (1961) provide examples where the scaling requirements have been met and yet negative variances are estimated.

It is generally accepted that genetic effects can be established by showing segregation, such that the variance of the F_2 should be larger than the variance of the F_1 (Mather, 1949). However, Bruell (1962) has shown that the variance of the F_2 generation may be smaller than expected. He states that the genetic variance of the F_2 is not always the largest among the three segregating generations as the relative size of the variances is a function of the degree of dominance. This dependency would produce relatively smaller variances in the backcross to the dominant parent and larger variances in the backcross to the recessive parent. This is seen to be generally true for the present study. Bruell also shows that genetic variance is inversely related to the number of segregating units controlling the character. That is, the larger the number of genetic factors involved, the smaller the genetic component of variance becomes. (A genetic factor is defined by Mather (1949) as a segment of chromosome acting as an unit of inheritance.) Segregation cannot be demonstrated when the genetic component of variance becomes

small relative to the environmental component. The effects
of both dominance and the number of genetic factors contribute
toward the inability to show segregation by the ratio V_{F_2}/V_e
as dominance has been shown to be present and many genetic
factors are probably involved in avoidance behavior.

The estimate of V_e is another major factor in that
experimental error is increased due to non-rigorous control
of identifiable factors which increase error. Bruell (1962)
stresses the importance of meticulous control of error
variance and suggests increasing the number of subjects to
reduce the standard error. Increasing the number of subjects
is probably effective only to a certain degree as it will not
decrease the error variance in a non-segregating generation
that is susceptible to small environmental fluctuations.

Detection of genetic variance by the classic method
is further altered by the violation of the assumptions of
isodirectionality of allelic effects and equality of additive
gene increments. The present study most probably violates
the first assumption as in the inbreeding process there is no
indication that selection was applied such that all the
increasing genetic factors be in some strains and all the
decreasing genetic factors for avoidance behavior be in other
strains. The effect of violation of this assumption cannot
be evaluated.

Estimates of the number of genetic factors involved were not reported. Newell (1970) writes,

> "Falconer has remarked that the use
> of the presently available formulas
> for estimating k are not really
> appropriate unless there is good
> evidence that the assumptions of
> isodirectional distribution of
> alleles and equality of additive
> gene increments have been met."

Newell (1970) cautions one to be skeptical of studies which freely estimate k values and construct theoretical models based on them. He points out that accurate estimation of k is a most complex and difficult undertaking and should not be attempted indiscriminately.

Henderson (1968) also states that "...although detailed procedures for obtaining precise genetic estimates are available, interpretation of these analyses beyond approximate quantitative or qualitative statements may be unwarranted." Wahlsten (1971) after critically reviewing the genetic experiments with animal learning suggests that avoidance behavior may be a too complex task and simpler learning tasks should be considered. He concludes that studies of complex learning are informative when the exper-imental question specifically involves the matter of complexity, but they otherwise confuse the issue of genetic control of learning by invoking numerous processes which are not involved in simple learning tasks. The present study seems to bear this out. No solution seems apparent for futher genetic

studies on avoidance behavior in mice. Working with known
mutants that might behave differently would be a slow process
involving many pleiotropic effects. Looking for mutations
centrally involved in avoidance behavior would be a laborious
task with much difficulty in distinguishing genotypes because
of the large variability of certain genotypes.

From the correlation matrices it can be seen that
activity as measured by the number of crossings over the
midline during intertrial intervals is associated with
avoidance behavior. Other factors which were not considered
may be even more centrally involved.

For more meaningful conclusions a parameter for non-
allelic interaction may need to be introduced as indicated by
the number of significant chi-squares in the classical analysis.
Estimation of this parameter is complicated by the presence
of genotype-environment interactions as evidenced by the
significant F_{max} ratios of the non-segregating generation
variances and by the fact that none of the transformations
improved the homogeneity of variances in the F_1 diallel
cross (Appendix III and Table 6). Another aspect of the
problem may stem from the manner in which avoidance behavior
is measured. The conditions used to measure avoidance
conditioning behavior may be creating a floor and ceiling
effect. That is, the conditions are such that differentiation
between levels of avoidance behavior cannot be made especially
within the very inferior or very superior avoidance learners.

In summary, the genetic analyses of avoidance behavior in 2,204 mice belonging to the inbred strains, A/HeJ, BALB/cJ, SWR/J and 129/J and to the F_1, F_2 and backcross generations was carried out. The results show a difference for males and females. Females score significantly higher than males in the number of correct avoidances, have smaller estimates of variation due to dominance effects, larger estimates of variation due to additive effects and as a consequence have higher heritabilities and a lower mean degree of dominance. For males the overall mode of inheritance is that of strong overdominance, whereas, for females all modes of inheritance are displayed. Examination of individual crosses shows that the mode of inheritance varies with the strains used such that a given strain will exhibit strong overdominance in one cross and partial dominance in another.

Non-allelic and genotype-environment interactions were found to be present. A transformation could not be found to eliminate these interactions and the extent of their effect on the analyses cannot be evaluated.

An attempt was undertaken to obtain estimates of genetic parameters but because of the complexity of the behavior, precise explanation of genetic effects could not be found. Genetic effects are more pronounced on day one and this may reflect that initial response to noxious stimuli is of more adaptive value than learning to increase avoidance to stimuli already in the mouse's repertoire.

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APPENDIX I

Tables of means (bold type) and variances (italics) for each day for males and females along with the variance of each array, V_r, the covariance, W_r, of each array with the parental strains, and the difference between the variance and covariance of each array.

Code for the diallel crosses:

        1   A/HeJ

        2   BALB/cJ

        3   SWR/J

        4   129/J

F_1

					W_r	V_r	$W_r - V_r$
1	3.67 *20.42*	2.20 *4.40*	12.33 *31.52*	2.36 *4.25*	12.03	17.34	-5.32
2	4.33 *22.24*	2.89 *9.99*	14.09 *43.49*	1.91 *5.89*	16.41	31.23	-14.82
3	9.87 *12.98*	14.00 *9.17*	9.16 *26.38*	6.89 *15.11*	-3.44	6.19	-9.63
4	1.30 *2.46*	3.10 *16.99*	10.10 *34.10*	3.33 *8.24*	8.64	9.19	-0.56

F_2

1	3.67 *20.42*	7.28 *41.10*	10.42 *31.99*	6.49 *30.30*	5.36	6.61	-1.25
2	7.33 *48.92*	2.89 *9.99*	12.69 *31.32*	7.36 *20.82*	10.24	14.59	-4.35
3	9.45 *27.40*	11.67 *30.22*	9.16 *26.38*	5.88 *25.09*	-0.77	6.04	-6.81
4	7.42 *33.20*	5.85 *30.82*	6.59 *29.63*	3.33 *8.24*	0.89	2.75	-1.86

MALES   DAY 1

F_1

					W_r	V_r	$W_r - V_r$
1	8.75 *32.20*	1.50 *4.06*	16.83 *31.24*	5.36 *23.86*	12.35	28.07	-15.72
2	9.07 *47.35*	7.39 *41.31*	18.27 *26.82*	10.45 *32.07*	12.60	33.81	-21.20
3	16.53 *14.27*	17.77 *10.19*	12.60 *39.05*	10.22 *42.19*	-3.52	9.22	-12.75
4	5.90 *7.43*	3.40 *28.49*	13.40 *16.49*	8.00 *28.91*	5.33	7.08	-1.75

F_2

1	8.75 *32.20*	8.79 *47.59*	15.34 *42.97*	9.94 *30.06*	5.35	6.47	-1.12
2	11.36 *37.36*	7.39 *41.31*	15.15 *33.27*	13.48 *30.29*	7.64	12.99	-5.35
3	13.60 *44.71*	16.80 *25.72*	12.60 *39.05*	10.98 *31.45*	-2.21	2.87	-5.08
4	9.43 *37.10*	10.19 *31.51*	13.79 *37.96*	8.00 *28.91*	2.46	4.09	-1.63

MALES   DAY 2

F_1					W_r	V_r	W_r-V_r
1	11.67 *67.70*	3.50 *19.17*	16.00 *37.45*	9.73 *50.22*	12.27	18.48	-6.21
2	12.80 *72.17*	10.44 *66.73*	19.18 *10.96*	16.27 *17.22*	12.78	24.30	-11.52
3	20.47 *5.27*	19.92 *9.41*	16.77 *30.28*	15.56 *20.28*	-1.18	4.64	-5.81
4	11.60 *28.71*	8.20 *43.96*	13.50 *41.17*	11.00 *26.73*	4.31	3.06	1.25

F_2	·						
1	11.67 *67.70*	10.92 *63.02*	16.57 *49.34*	12.73 *40.45*	5.54	3.84	1.70
2	12.94 *61.93*	10.44 *66.73*	17.52 *25.78*	15.48 *30.69*	7.94	9.16	-1.22
3	14.98 *47.12*	17.37 *24.82*	16.77 *30.28*	12.30 *41.19*	1.27	2.53	-1.26
4	11.28 *41.16*	12.30 *36.26*	15.28 *25.68*	11.00 *26.73*	1.78	1.99	-0.21

MALES DAY 3

F_1					W_r	V_r	W_r-V_r
1	24.08 *203.72*	7.20 *57.07*	45.17 *245.06*	17.45 *117.27*	110.71	184.20	-73.48
2	26.20 *315.31*	20.72 *227.98*	51.54 *136.87*	28.64 *117.86*	126.63	259.34	-132.76
3	46.87 *20.98*	51.69 *66.23*	38.53 *179.97*	32.67 *162.75*	-25.63	56.59	-82.21
4	18.80 *67.96*	14.70 *170.23*	37.00 *162.22*	22.33 *138.24*	55.02	53.28	1.74

F_2							
1	24.08 *203.72*	27.00 *359.53*	42.34 *237.58*	29.16 *175.72*	48.87	46.58	2.29
2	31.64 *265.11*	20.72 *227.98*	45.36 *168.24*	36.33 *154.54*	78.00	106.54	2.29
3	38.02 *258.08*	45.85 *165.46*	38.53 *179.97*	29.16 *174.63*	-6.38	29.50	-35.88
4	28.13 *216.96*	28.34 *216.66*	35.67 *157.91*	22.33 *138.24*	16.81	22.44	-5.63

MALES TOTAL

F_1

					W_r	V_r	W_r-V_r
1	5.29 *35.22*	7.50 *35.36*	9.64 *19.32*	4.36 *19.65*	9.98	11.69	-1.70
2	3.23 *17.53*	5.90 *22.94*	15.80 *18.40*	3.18 *4.56*	15.60	29.01	-13.41
3	13.07 *20.21*	15.17 *14.88*	10.26 *23.35*	8.50 *30.50*	1.22	9.38	-8.16
4	2.70 *3.12*	3.77 *12.86*	7.92 *21.17*	3.23 *11.41*	6.68	5.77	0.91

F_2

					W_r	V_r	W_r-V_r
1	5.30 *35.22*	6.37 *30.77*	11.67 *28.72*	5.60 *31.74*	5.89	5.02	0.87
2	8.71 *38.86*	5.90 *22.94*	13.41 *35.00*	10.40 *34.36*	6.30	10.66	-4.36
3	9.22 *34.77*	13.54 *30.30*	10.26 *23.35*	8.56 *36.77*	2.14	5.52	-3.38
4	6.88 *36.04*	8.63 *35.00*	6.90 *25.69*	3.23 *11.42*	4.69	7.09	-2.39

FEMALES   DAY 1

F_1

					W_r	V_r	W_r-V_r
1	8.88 *69.24*	9.92 *71.54*	15.64 *21.17*	8.27 *32.62*	13.54	16.41	-2.86
2	8.23 *25.53*	11.15 *33.92*	18.00 *5.11*	12.18 *11.56*	14.86	20.37	-5.51
3	17.47 *18.12*	20.58 *7.17*	16.13 *26.38*	11.20 *36.84*	1.63	5.28	-3.65
4	7.10 *14.54*	10.31 *22.56*	16.17 *22.33*	8.73 *44.59*	8.86	7.21	1.65

F_2

					W_r	V_r	W_r-V_r
1	8.88 *69.24*	9.74 *63.43*	16.28 *22.25*	9.17 *45.80*	8.19	6.10	2.10
2	12.34 *62.00*	11.15 *33.92*	16.20 *18.96*	14.46 *22.41*	6.51	6.00	0.51
3	13.13 *39.06*	16.29 *39.97*	16.13 *26.38*	13.36 *44.98*	4.39	3.58	0.81
4	11.69 *37.65*	12.43 *47.29*	11.00 *27.60*	8.73 *44.59*	4.21	4.24	-0.03

FEMALES   DAY 2

F_1					W_r	V_r	W_r-V_r
1	8.88	11.75	17.28	9.64	15.39	18.48	-3.09
	65.61	*65.11*	*34.07*	*29.26*			
2	14.38	14.30	18.40	16.00	9.51	7.86	1.65
	51.42	*39.90*	*37.38*	*11.40*			
3	20.33	20.58	18.02	13.60	-0.64	1.74	-2.39
	7.95	*9.36*	*18.73*	*15.16*			
4	12.00	13.92	19.25	13.14	8.93	5.86	3.08
	50.44	*38.91*	*10.57*	*32.70*			

F_2							
1	8.88	10.77	18.39	12.74	12.12	10.87	1.25
	65.61	*50.48*	*20.49*	*55.51*			
2	13.94	14.30	16.92	15.86	6.95	3.88	3.07
	57.11	*39.90*	*17.87*	*30.00*			
3	15.47	16.19	18.02	15.45	1.90	1.34	0.56
	35.81	*46.45*	*18.73*	*28.81*			
4	13.18	14.92	15.02	13.14	3.93	1.73	2.02
	36.48	*38.11*	*40.07*	*32.70*			

FEMALES   DAY 3

F_1					W_r	V_r	W_r-V_r
1	23.06	29.17	42.57	22.27	108.51	132.41	-23.89
	440.18	*398.15*	*121.34*	*192.42*			
2	25.85	31.35	52.20	31.36	116.05	155.66	-39.62
	212.81	*202.03*	*79.29*	*53.06*			
3	50.87	56.33	44.41	33.30	7.10	43.46	-36.36
	82.70	*39.15*	*93.49*	*158.68*			
4	21.80	28.00	43.33	25.09	67.86	50.28	17.58
	127.07	*132.33*	*115.15*	*165.13*			

F_2							
1	23.06	26.88	46.35	27.51	73.27	62.34	10.93
	440.18	*383.46*	*105.36*	*265.79*			
2	35.00	31.35	46.53	40.73	56.41	55.31	1.10
	327.94	*202.03*	*129.30*	*163.30*			
3	37.82	47.02	44.41	37.38	24.62	25.15	-0.54
	234.22	*224.32*	*93.49*	*194.80*			
4	31.75	35.98	32.93	25.09	34.72	34.56	0.16
	203.92	*228.34*	*199.57*	*165.13*			

FEMALES   TOTAL

APPENDIX II

Graphs for days one, two and three of the inverse probability integral of the cumulative sum,p, of the percentage frequencies up to each class limit.

Code for the crosses:

        ■   A/HeJ

        ●   BALB/cJ

        ▲   SWR/J

        £   129/J

        $ A/HeJ x BALB/cJ

        1   A/HeJ x SWR/J

        c   A/HeJ x 129/J

        0   BALB/cJ x SWR/J

        △   BALB/cJ x 129/J

        □   SWR/J x 129/J

DAY 1

number of correct avoidances

DAY 2
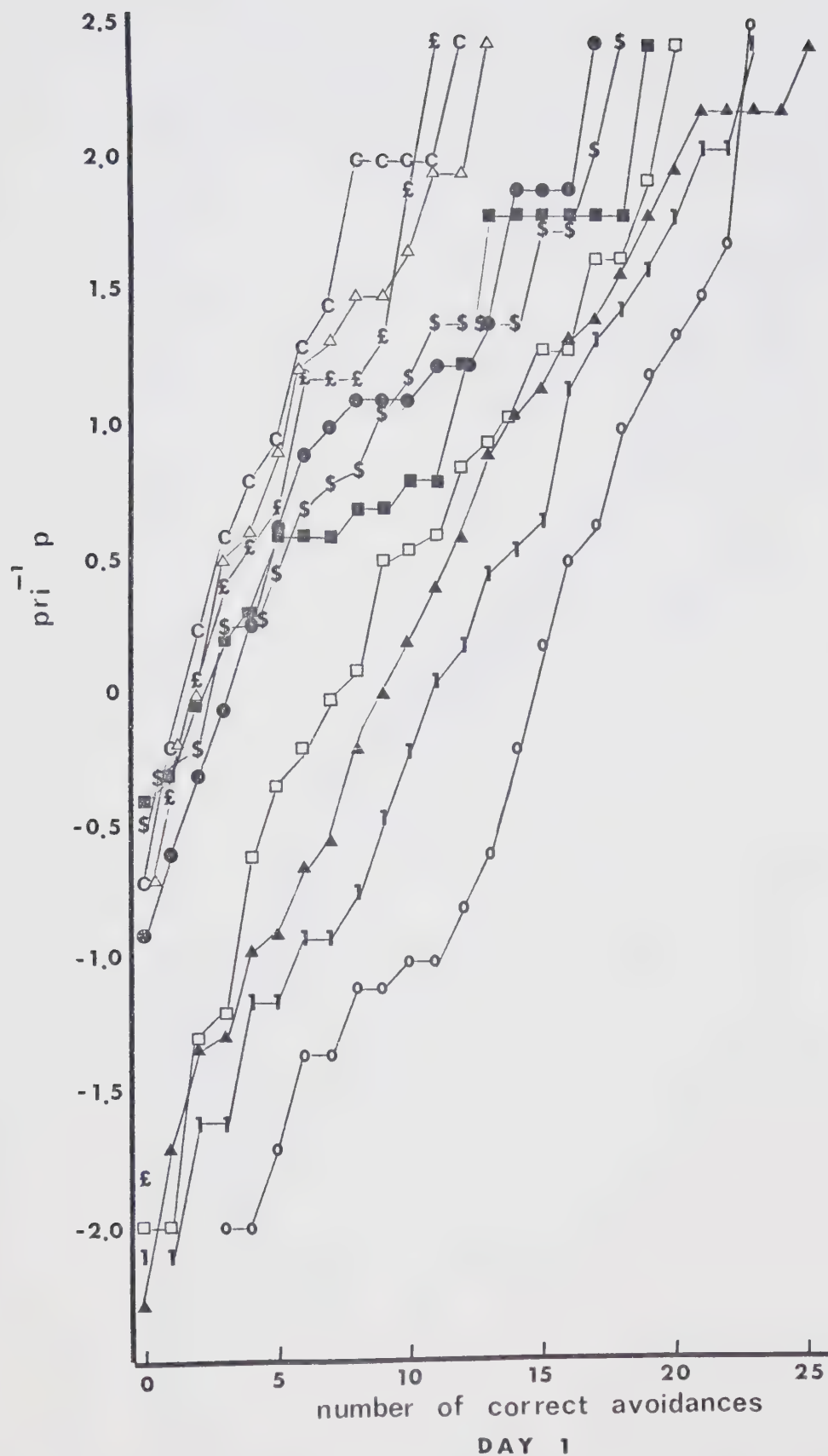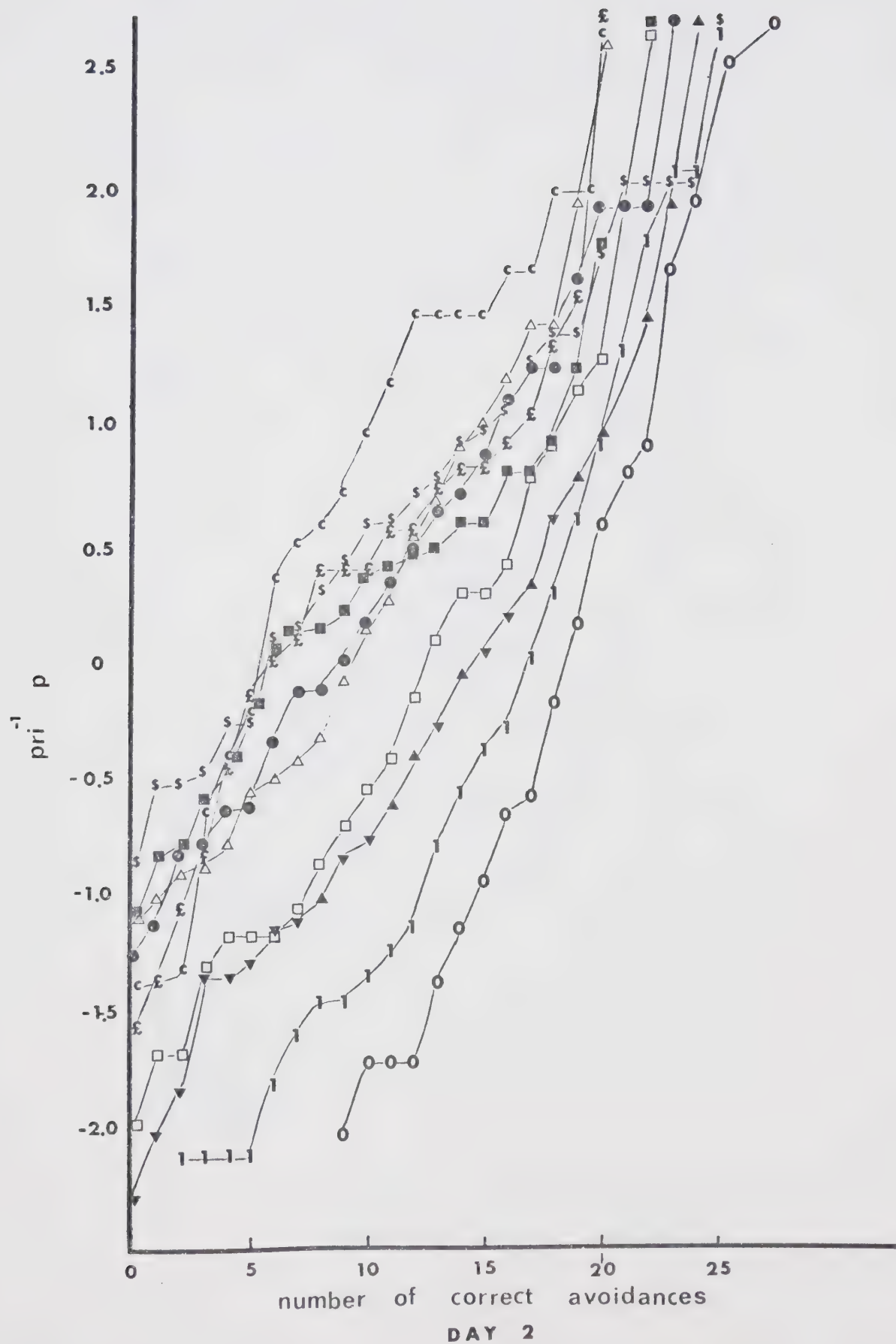
DAY 3

APPENDIX III

Results from classical analysis:

The upper part of each table presents the mean and variance for each of the generation groups for each day. The lower part of the table presents the statistics in the text.

Sexes combined, reciprocals combined

	N	DAY 1		DAY 2		DAY 3		TOTAL	
P_1	29	4.62	28.82	8.83	52.22	10.03	66.03	23.48	355.40
P_2	89	9.73	24.84	14.43	35.27	17.42	24.43	41.57	142.43
F_1	56	11.20	21.65	16.62	19.95	18.68	22.58	46.50	113.64
F_2	196	10.17	31.54	14.54	38.10	16.36	38.78	41.08	217.00
B_1	48	10.62	34.79	14.00	46.21	17.38	35.60	42.00	252.38
B_2	45	9.09	27.31	15.58	31.11	17.84	30.72	42.51	168.12
m		7.96 ± 0.94**		12.09 ± 0.35**		14.64 ± 0.93**		34.98 ± 2.00**	
d		1.60 ± 0.98		2.36 ± 0.38**		2.61 ± 0.96*		6.28 ± 2.10*	
h		3.66 ± 1.64*		4.73 ± 0.57**		4.14 ± 1.53**		11.98 ± 3.21**	
chi-square		11.62**		1.12		7.58		6.22	
V_e		24.47		33.16		30.77		168.66	
V_d		0.99		-1.13		11.22		13.51	
V_h		6.08		6.07		-3.22		34.84	
heritability		0.03		–		–		0.06	
$(V_h/V_d)^{1/2}$		2.48		–		–		1.61	
(V_t/V_e)		1.29		1.15		1.26		1.29	
$F_{max}(P_1/P_2)$		1.16		1.48		2.70**		2.50**	
$F_{max}(P_1/F_1)$		1.33		2.62**		2.92**		3.13**	
$F_{max}(P_2/F_1)$		1.15		1.77*		1.08		1.25	

Sexes combined, Reciprocals separate

	N	DAY 3	
P_1	29	10.03	66.03
P_2	89	17.42	24.43
F_1	30	20.40	6.39
F_2	100	15.27	40.26
B_1	23	15.26	41.38
B_2	33	18.39	34.62
m		12.96 ± 0.88**	
d		4.21 ± 0.93**	
h		7.13 ± 1.18**	
chi-square		5.65	
V_e		28.92	
V_d		4.51	
V_h		6.82	
heritability		0.11	
$(V_h/V_d)^{1/2}$		1.23	
(V_t/V_e)		1.39	
$F_{max}(P_1/P_2)$		2.70**	
$F_{max}(P_1/F_1)$		10.34**	
$F_{max}(P_2/F_1)$		3.82**	

Sexes separate; reciprocals combined

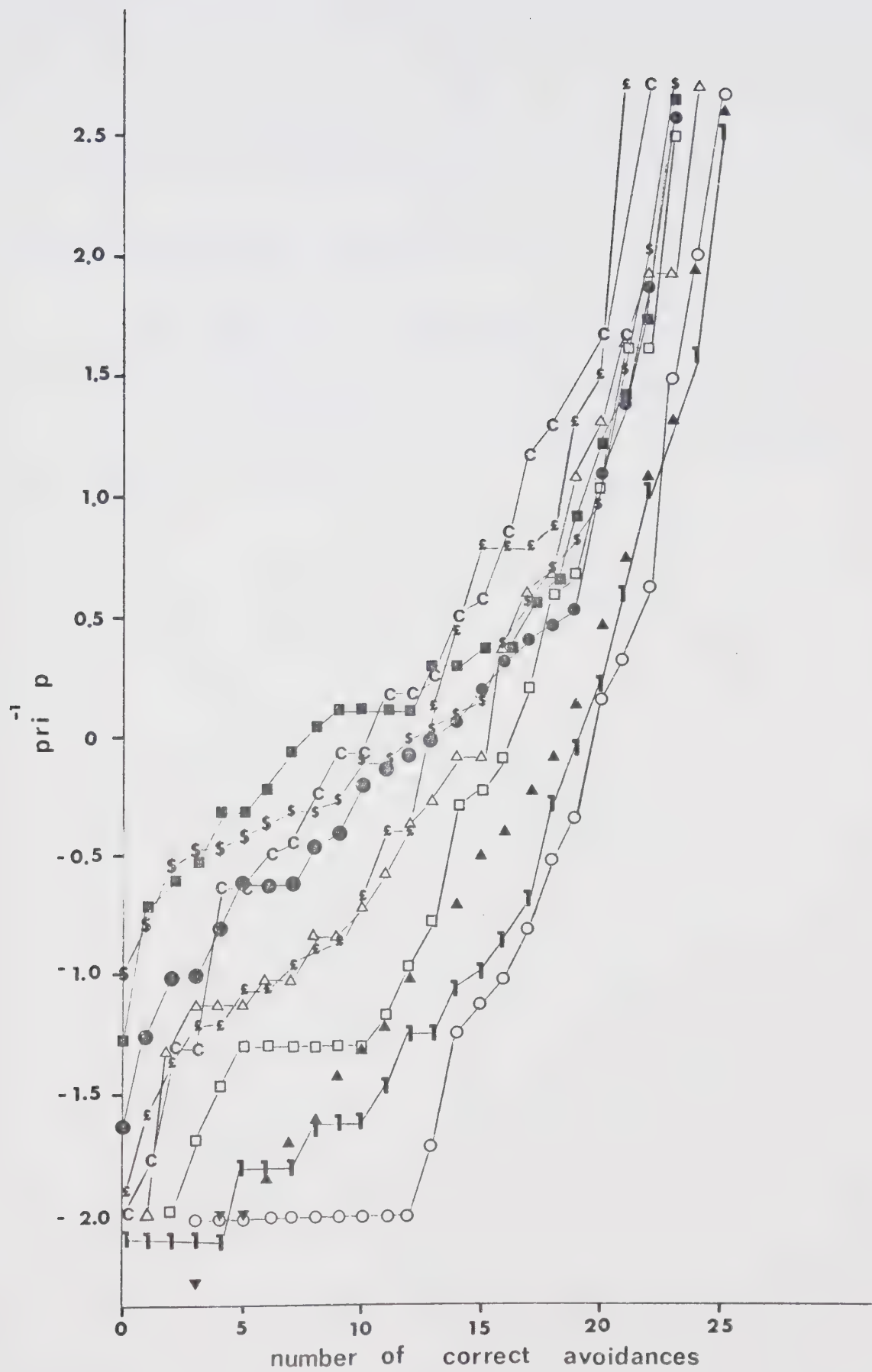|	N	DAY 1 Females		N	TOTAL Males	
P_1	17	5.29	35.22	12	24.08	63.72
P_2	46	10.26	23.35	43	38.53	79.97
F_1	29	11.41	22.11	27	46.11	115.72
F_2	109	10.32	32.96	87	40.36	248.79
B_1	26	9.35	28.23	22	43.50	310.64
B_2	26	9.19	32.32	19	43.16	135.03
m		3.25 ± 0.71**			32.15 ± 1.52**	
d		1.86 ± 0.74*			6.47 ± 1.56**	
h		3.32 ± 1.26*			15.40 ± 2.85**	
chi-square		3.39			4.20	
V_e		25.15			89.36	
V_d		5.36			51.91	
V_h		2.44			107.52	
heritability		0.16			0.21	
$(V_h/V_d)^{1/2}$		0.68			1.44	
(V_t/V_e)		1.31			2.78**	
$F_{max}(P_1/P_2)$		1.51			1.25	
$F_{max}(P_1/F_1)$		1.59			1.82	
$F_{max}(P_2/F_1)$		1.06			1.45	

A/HeJ (P_1) x SWR/J (P_2)

	N	DAY 1		DAY 2		DAY 3		TOTAL	
P_1	38	4.47	18.69	9.37	40.02	12.47	54.96	26.32	237.41
P_2	89	9.73	24.84	14.43	35.27	17.42	24.43	41.57	142.43
F_1	46	14.72	19.98	18.67	12.80	19.59	15.36	52.98	77.62
F_2	195	12.84	31.77	16.09	26.39	17.25	28.26	46.18	169.35
B_1	49	8.86	37.25	13.28	45.70	16.42	39.67	38.57	269.29
B_2	50	11.50	39.15	14.90	33.72	16.34	34.60	42.74	240.56
m		7.51 ± 0.97**		12.17 ± 0.82**		15.03 ± 0.71**		35.01 ± 2.18**	
d		2.53 ± 1.00*		2.21 ± 0.90*		2.06 ± 0.76*		6.63 ± 2.35*	
h		8.14 ± 1.84**		6.63 ± 1.34**		4.27 ± 1.19**		18.59 ± 3.61**	
chi-square		17.52**		8.46*		5.82		10.81*	
V_e		22.20		30.34		28.72		146.06	
V_d		-12.85		-26.70		-17.74		-171.15	
V_h		22.43		22.74		17.28		194.44	
heritability									
$(V_h/V_d)^{\frac{1}{2}}$		-		-		-		-	
(V_t/V_e)		1.43*		0.87		0.98		1.16	
F_{max} (P_1/P_2)		1.33		1.13		2.25**		1.67	
F_{max} (P_1/F_1)		1.07		3.13**		3.58**		3.06**	
F_{max} (P_2/F_1)		1.24		2.76**		1.59		1.83*	

BALB/cJ (P_1)   x   SWR/J (P_2)

Sexes combined, Reciprocals separate

	N	DAY 1		DAY 2		DAY 3		TOTAL	
P_1	34	3.26	10.02	8.47	38.14	12.38	30.79	24.12	152.96
P_2	89	9.73	24.84	14.43	35.27	17.42	24.43	41.57	142.43
F_1	41	0.36	24.69	12.98	32.17	15.66	25.73	37.00	156.10
F_1	105	7.05	30.32	12.29	37.08	14.47	35.22	33.81	190.26
F_2	38	2.95	9.52	10.42	33.55	13.50	33.23	26.87	146.17
B_1	95	8.86	27.12	14.67	32.07	17.61	24.71	41.15	153.40
B_2									

	DAY 1	DAY 2	DAY 3	TOTAL
m	6.19 ± 0.90**	11.43 ± 0.43**	14.6- ± 0.72**	32.10 ± 1.41**
d	3.83 ± 0.86**	3.31 ± 0.42**	3.07 ± 0.71*	10.09 ± 1.38**
h	0.98 ± 1.89	1.93 ± 0.80*	1.06 ± 1.34	4.61 ± 2.71
chi-square	19.26**	1.84	6.70	4.89
V_e	21.73	35.09	26.07	148.03
V_d	24.02	8.53	12.50	80.95
V_h	-15.42	-6.54	-3.35	-38.72
heritability	-	-	-	-
$(V_h/V_d)^{\frac{1}{2}}$	1.40*	-	-	-
(V_t/V_e)	-	1.06	1.35	1.28
F_{max} (P_1/P_2)	2.48**	1.08	1.26	1.07
F_{max} (P_1/F_1)	2.46**	1.18	1.20	1.02
F_{max} (P_2/F_1)	1.01	1.10	1.05	1.10

Sexes combined, Reciprocals separate — DAY 3

N	DAY 3	
34	12.34	30.79
89	17.42	24.43
19	14.53	31.77
105	13.95	32.66
28	13.86	53.39
27	16.56	11.67

	DAY 3
m	14.82 ± 0.38**
d	2.54 ± 0.39**
h	-0.58 ± 0.78
chi-square	1.75
V_e	25.04
V_d	4.10
V_h	7.74
heritability	0.11
$(V_h/V_d)^{\frac{1}{2}}$	0.32
(V_t/V_e)	1.30
F_{max} (P_1/P_2)	1.26
F_{max} (P_1/F_1)	1.75
F_{max} (P_2/F_1)	1.39

Sexes separate; reciprocals combined

N	DAY 2 Females		N	DAY 3 Males	
22	8.73	44.59	12	11.00	26.73
46	16.13	26.38	43	16.77	30.28
22	13.91	33.90	19	14.47	30.47
96	12.35	38.57	89	13.61	36.24
20	11.35	34.03	18	11.83	39.91
45	14.58	38.11	50	17.54	26.99

	DAY 2 Females	DAY 3 Males
m	12.23 ± 0.38**	13.55 ± 1.09**
d	3.74 ± 0.37**	3.81 ± 1.06**
h	1.06 ± 0.73	1.45 ± 2.01
chi-square	0.83	5.87
V_e	32.67	29.81
V_d	4.99	5.58
V_h	0.90	0.85
heritability	0.13	0.15
$(V_h/V_d)^{\frac{1}{2}}$	0.42	0.39
(V_t/V_e)	1.18	1.22
F_{max} (P_1/P_2)	1.69	1.13
F_{max} (P_1/F_1)	1.32	1.15
F_{max} (P_2/F_1)	1.28	1.01

129/3 (P_1) × SWR/3 (P_2)

	N	DAY 1			DAY 2			DAY 3			TOTAL	
P_2	38	4.47	18.69	P_1	8.83	52.22	P_1	10.03	66.03	P_1	23.48	355.40
P_1	29	4.62	28.82	P_2	9.37	40.02	P_2	12.47	54.96	P_2	26.32	237.41
F_1	56	4.38	23.10		7.54	46.25		11.10	66.99		23.02	307.61
F_2	142	7.42	39.66		10.50	53.51		12.10	58.81		30.02	330.69
B_2	50	6.40	33.92	B_1	10.25	56.74	B_1	10.83	69.71	B_1	26.71	353.58
B_1	52	5.63	25.76	B_2	8.58	49.39	B_2	13.12	54.52	B_2	28.10	315.89

	DAY 1	DAY 2	DAY 3	TOTAL
m	$5.72 \pm 1.31^{**}$	$10.20 \pm 1.10^{**}$	$11.74 \pm 0.56^{**}$	$27.84 \pm 2.86^{**}$
d	0.21 ± 1.34	0.43 ± 1.13	$1.44 \pm 0.57^{*}$	0.68 ± 2.94
h	0.05 ± 2.26	-1.53 ± 1.92	0.07 ± 1.01	-1.28 ± 5.05
chi-square	19.32^{**}	7.13	1.42	7.51
V_e	23.08	45.74	63.05	297.19
V_d	19.64	0.90	-6.60	-8.09
V_h	-3.06	6.88	2.37	41.59
heritability	—	0.02	—	—
$(V_h/V_d)^{\frac{1}{2}}$	—	2.76	—	—
(V_t/V_e)	1.72^{*}	1.17	0.93	1.11
F_{max} (P_1/P_2)	1.54	1.30	1.20	1.50
F_{max} (P_1/F_1)	1.25	1.13	1.22	1.30
F_{max} (P_2/F_1)	1.24	1.16	1.01	1.16

A/HeJ (P_1) x   BALB/cJ (P_2)

	N	DAY 1		DAY 2			DAY 3			TOTAL		
P_1	34	3.26	10.02	P_1	8.47	38.14	P_2	10.03	66.03	P_2	23.48	355.40
P_2	29	4.62	28.82	P_2	8.83	52.22	P_1	12.38	30.79	P_1	24.12	152.96
F_1	42	2.71	8.31		6.67	19.94		10.69	37.93		20.07	122.60
F_2	223	6.64	32.99		10.10	38.29		12.47	43.10		29.20	215.81
B_1	46	4.00	19.42	B_1	10.24	40.01	B_2	11.85	47.38	B_2	26.09	214.44
B_2	94	7.21	37.05	B_2	12.70	54.94	B_1	13.66	49.69	B_1	33.57	320.48

	DAY 1	DAY 2	DAY 3	TOTAL
m	6.26 ± 1.66*	11.34 ± 1.87**	12.74 ± 1.16**	30.90 ± 4.39**
d	2.23 ± 1.75	1.59 ± 2.02.	-0.32 ± 1.16	4.54 ± 4. 6
h	-2.27 ± 2.64	-3.06 ± 3.17	-0.83 ± 2.16	-6.56 ± 7.58
chi-square	42.26**	25.41**	8.27*	25.07**
V_e	14.52	34.74	43.38	196.73
V_d	9.50	-18.38	-10.87	-103.30
V_h	8.96	21.92	10.59	122.38
heritability	0.29	—	—	—
$(V_h/V_d)^{\frac{1}{2}}$	0.97	—	—	—
(V_t/V_e)	2.27**	1.10	0.99	1.10
F_{max} (P1/P2)	2.88**	1.37	2.14*	2.32*
F_{max} (P1/F1)	1.21	1.91	1.74	1.25
F_{max} (P2/F1)	3.47**	2.62*	1.23	2.90**

129/J (P_1) x A/HeJ (P_2)

	N	DAY 1		DAY 2		DAY 3		TOTAL	
P_1	34	3.26	10.02	8.47	38.14	12.38	30.70	24.12	152.96
P_2	38	4.47	18.69	9.37	40.02	12.47	54.96	26.32	237.41
F_1	45	3.02	9.84	9.27	32.52	13.73	35.97	26.02	148.89
F_2	202	8.11	32.53	12.70	34.80	14.70	35.05	35.51	206.48
B_1	65	4.00	24.53	9.23	42.15	11.45	47.16	24.68	239.85
B_2	116	6.16	25.69	12.78	46.55	14.14	46.12	33.09	250.36
m		5.65 ± 1.98*		10.87 ± 2.02**		13.16 ± 1.25**		30.18 ± 5.27**	
d		1.30 ± 2.00		1.45 ± 1.98		0.88 ± 1.22		3.67 ± 5.25	
h		−0.73 ± 3.41		1.02 ± 3.72		1.35 ± 2.34		1.56 ± 9.58	
chi-square		82.86**		32.48**		11.87**		45.26**	
V_e		12.77		36.59		40.63		178.82	
V_d		14.84		−19.11		−23.18		−77.24	
V_h		4.92		17.32		17.60		104.90	
heritability		0.61		–		–		–	
$(V_h/V_d)^½$		0.57		–		–		–	
(V_t/V_e)		2.55**		0.95		0.86		1.15	
F_{max} (P_1/P_2)		1.86		1.05		0.86		1.15	
F_{max} (P_1/F_1)		1.02		1.17		1.78		1.55	
F_{max} (P_2/F_1)		1.90		1.23		1.17		1.03	

129/J (P_1)   x   BALB/cJ (P_2)

APPENDIX IV

Code for the variables in the correlation matrices:

1. Weight on first day of testing (40 ± 3 days of age).

2. Litter size.

3. Number of correct avoidances on day one.

4. Number of correct avoidances on day two.

5. Number of correct avoidances on day three.

6. Number of crossings of the midline during intertrial intervals on day one.

7. Number of crossings of the midline during intertrial intervals on day two.

8. Number of crossings of the midline during intertrial intervals on day three.

9. Age of sire on day of birth.

10. Age of dam on day of birth.

	2	3	4	5	6	7	8	9	10
1	-0.229**	-0.163**	-0.181**	-0.142**	-0.082	-0.044	-0.005	0.020	0.092
2		0.168**	-0.005	-0.019	0.021	0.007	-0.055	0.097	-0.0122*
3			0.663**	0.500**	0.297**	0.258**	0.240**	0.093	-0.047
4				0.714**	0.322**	0.301**	0.276**	0.100*	-0.000
5					0.215**	0.206**	0.255**	0.060	0.041
6						0.525**	0.492**	0.166**	-0.001
7							0.559**	0.126*	0.081
8								0.051	0.010
9									0.297**

** p < 0.005
* p < 0.025

Correlation matrix for F_1 diallel cross.

	2	3	4	5	6	7	8	9	10
1	-0.217**	-0.036	-0.023	-0.017	0.022	0.049	0.053	0.100**	0.129**
2		0.003	-0.012	-0.007	0.055	0.018	-0.010	-0.086**	-0.106**
3			0.538**	0.440**	0.159**	0.143**	0.127**	0.087**	0.076*
4				0.660**	0.175**	0.294**	0.251**	0.118**	0.114**
5					0.177**	0.201**	0.225**	0.072*	0.067*
6						0.448**	0.425**	0.110***	0.071*
7							0.640**	0.142**	0.140**
8								0.143**	0.140**
9									0.925**

**   p < 0.005
*   p < 0.025

Correlation matrix for F_2 diallel cross.

	2	3	4	5	6	7	8	9	10
1	-0.289**	-0.072	-0.011	0.013	0.020	0.053	0.040	0.001	0.133**
2		0.093*	-0.005	0.000	0.055	-0.040	0.051	0.019	-0.284**
3			0.625**	0.477**	0.133**	0.172**	0.115**	-0.009	0.126**
4				0.706**	0.155**	0.264**	0.156**	-0.047	0.105*
5					0.082	0.112*	0.142**	-0.051	0.020
6						0.516**	0.435**	-0.004	0.061
7							0.571**	0.068	0.139*
8								0.047	0.079
9									0.085

** $p < 0.005$

* $p < 0.025$

Correlation matrix for backcrosses.